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VALIDITY OF MAIL SURVEY DATA ON BAGGED WATERFOWL

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INTRODUCTION

In 1951, an analysis was made of the judgment sampling method then used by the Fish and Wildlife Service to estimate the kill of waterfowl by hunters. The study revealed the sample data to be seriously distorted by bias errors resulting from methods used in selecting the sample.

A post-season mail survey for estimating the kill of upland game and waterfowl by hunters has been carried out in Indiana since 1944 by Barnes (1946). Subsequently a number of other state game departments began sampling hunters by systems amenable to statistical analysis.

While the question of validity of data from mail surveys of hunters was raised much earlier, specific information was not published until Hjersman (1951) in California and Nelson (1951) in Utah reported that such data always contain a positive error. Nelson also reported that the positive error was consistent during the 1948–1950 period covered by his report. In addition, G. H. Jensen (unpublished report of U. S. Fish and Wildlife Service, 1951) has summarized results of a post-season mail survey of a sample of hunters who hunted more than once on the Public Hunting Area of Bear River National Waterfowl Refuge in Utah, during the 1950 waterfowl season. The survey data when compared to the actual kill data likewise showed a positive error both with respect to the seasonal waterfowl kill reported and in the number of times afield.

After examining these three reports it seemed desirable to obtain more information on the method before it was adopted by the Fish and Wildlife Service as being suitable for fulfilling the validity desired. This paper summarizes results of a preliminary investigation carried out prior to the development of a sampling plan for estimating annual hunter-kill of waterfowl in the United States.

Sincere appreciation for excellent cooperation is extended to all personnel of the Missouri Conservation Department who were connected with this study, especially Harold Terrill and Charles Shanks for coordination and field supervision efforts. Grateful appreciation is also extended to Allen G. Smith and G. Hortin Jensen, U. S. Fish and Wildlife Service, for supervising and carrying out field contacts at Lower Klamath and Bear River study areas.

The investigation was designed to obtain information to satisfy the following objectives:

1. To determine the total error in shot and retrieved waterfowl questionnaire reports after one, two and three post-season mail contacts.
2. To determine the error in post-season questionnaire reports of hunters concerning the species of waterfowl retrieved. (To be discussed in a later report.)
3. To determine whether serious bias errors occur in post-season reports of waterfowl shot and retrieved.
4. To devise a reliable method for removing the effect of a sufficient proportion of the bias error to reduce total errors to reasonable and predictable limits, if serious bias or biases are detected and identified.

STUDY AREAS

Provision was made to obtain data from at least two areas where contrasting hunter-success ratios occur. This provided data which could be examined for evidence of correlation between bias error and hunter-success and permitted a rough measure of the range of errors if bias error were detected.

In addition to these considerations certain

criteria, as follows, were necessary to provide satisfactory data from each study area:

1. The area must be well-known by waterfowl hunters in the state, have well-marked or natural boundaries, and be open to the public.
2. The management history of the area must be free of educational campaigns designed to increase the hunters ability to identify waterfowl, to reduce crippling losses, or to so condition the hunters using the area that they will be atypical of hunters at large.
3. The total numbers using the area must be at least 1,000 and preferably a larger number to permit valid statistical study.
4. The hunting management of the area must provide for controlling entry and exit of all hunters, so that kill figures can be obtained for comparison with reports in post-season questionnaires.

Relatively few public hunting areas qualify for consideration as study areas under the above criteria. One of these is the 12,000-acre Bear River Public Hunting Area in Utah, and another is the 7,000-acre Lower Klamath Public Hunting Area in northern California.

Field operations on these two areas began with the opening of the waterfowl hunting season in 1951, and two additional study areas were added in 1952. Both of the latter are game management areas owned and managed by the Missouri State Conservation Department as public hunting areas. One, the Fountain Grove Public Hunting Area is 3,433 acres in size and has approximately 1,758 acres open to hunting. Waterfowl hunting was first permitted on this area during the 1948 season. The second, the Trimble Public Hunting Area, consists of 776 acres and was opened to hunting in 1952.

METHODS OF STUDY

During the 1951–52 waterfowl season each hunter passed through a checking station at the completion of his hunt. At this contact his kill for the day was counted and recorded by species, and a record was made of his name, home address and hunting license number. Data from subsequent hunts on the area were recorded on cards on file at the checking stations. In addition, every fifth hunter was interviewed to determine the number of ducks, geese and coots knocked down within his sight, but not retrieved.

Identical questionnaire forms were used in contacting the hunters of record for each study area. The original contact questionnaire was mailed from the public hunting ground to hunters of records. The second and third contact questionnaires were mailed from the Fish and Wildlife Service office at Laurel, Maryland, where all returned questionnaires were processed.

During 1952 only an original and one follow-up questionnaire were mailed, both from the Laurel, Maryland office. During both seasons the original mail contact was 100 per cent of the hunters using the study areas.

Copies of original, follow-up letter and questionnaire form used are as follows:

Fellow Sportsmen:

The Fish and Wildlife Service is carrying on an investigation on selected public hunting areas for the purpose of getting information which can be used to improve our method of measuring the hunters kill of waterfowl. This information in turn, will permit better management and better utilization of this valuable natural resource.

The cover sheet which accompanied the "Migratory Waterfowl Hunter Registration Form" that you filled out the first time you were checked through the station at Fountain Grove Public Hunting area informed you that you would receive a questionnaire following the waterfowl season. The form on the other side of this sheet is the questionnaire previously referred to.

Please fill out the questionnaire and return it immediately in the enclosed self-addressed envelope which does not require postage. If you were one of the unlucky ones who hunted but killed no birds; please fill out the form anyway because such information is as important as that from successful hunters in determining the waterfowl kill.

We have a record of the actual kill on the Fountain Grove Public Hunting Area, and this information, together with what you will submit, will permit us to determine how accurately hunters can report their season's kill at the end of the season. This type of evaluation is necessary before we can enlarge our sampling areas to measure the national kill of waterfowl.

We appreciate your efforts and interest in improving waterfowl management through your cooperation in providing this information.

Sincerely yours,

Albert M. Day
Director
Fish and Wildlife Service

Fellow Sportsmen:

About three weeks ago we sent you a questionnaire form asking that you report on the results of your hunting during the past waterfowl hunting season. Inasmuch as your report has not been received to date, and with the belief that it may have been mislaid, we have duplicated the previous questionnaire on the other side of this form. You are again urged to complete the form to the best of your recollection, and to mail it in the self-addressed envelope which needs no postage.

We shall very much appreciate your giving attention to this today, since your report is an important contribution to the investigation.

Sincerely yours,
ALBERT M. DAY
Director
Fish and Wildlife Service

INSTRUCTIONS: Please fill out the form completely. Try to recall only what YOU killed and report only your hunting kill on the Fountain Grove Public Hunting Area. Do *not* report the kill of any other sportsman with whom you may have hunted.

1. Number of days during the past waterfowl hunting season you hunted for waterfowl?
   .....days.
2. Number of daily waterfowl hunting trips on which it was your ORIGINAL intention to hunt:
   For Ducks:..... For Geese:.....
   (trips) (trips)
   For Coots (Mud hens):.....
   (trips)
3. Total number of waterfowl bagged by YOU:
   Ducks:..... Geese:.....
   Coots (Mud hens):.....
4. Total number of waterfowl knocked down by YOU within your sight but NOT retrieved:
   Ducks:..... Geese:.....
   Coots (Mud hens):.....
5. Waterfowl bagged this season by you, that had leg bands .....
   (number)
   a. Band number:..... Date shot:.....
   b. Band number:..... Date shot:.....

RESULTS

More than one-third of the total sample was obtained within 21 days after the first mail contact (Table 1). The total was increased to 65 per cent within 21 days after the second contact was mailed (three weeks after the first), and to 78 per cent within 21 days after a third contact was mailed (six weeks after the original contact).

About 90 per cent of the total responses were received within an elapsed time of 21 days after being mailed to the sample of hunters and more than 95 per cent were returned within 30 days. The per cent of response is similar to that previously reported for systematically selected purchasers of state hunting licenses for waterfowl, upland and big game when both surveys included the same number of contacts and similar elapsed time after the contact.

TABLE 1.—QUESTIONNAIRE RESPONSES

Study Area	Mail Contact number	Per cent of return at cut-off date	Equivalent total response after 21 days, using n contacts
Lower Klamath, Calif., 1951	1	36.26[1]	35.02
	2	41.08	62.44
	3	47.32	80.21
Bear River, Utah, 1951	1	39.38[1]	34.29
	2	38.92	62.97
	3	35.99	76.30
Lower Klamath, Calif., 1952	1	38.57[2]	38.57[2]
	2	40.19	63.64
Bear River, Utah, 1952	1	41.24[3]	41.24[3]
	2	40.92	66.16
Fountain Grove, Mo., 1952	1	38.33[1]	38.33[1]
	2	46.03	67.44
Trimble, Mo., 1952	1	40.92[1]	40.92[1]
	2	43.52	67.20
Average Response	1	39.12[4]	.....
	2	41.78[4]	64.98
	3	41.66[4]	78.26

[1] 42 days after first mailing date.
[2] 48 days after first mailing date.
[3] 45 days after first mailing date.
[4] 42–48 days after first mailing date.

Data from all hunters on each study area were available and these were studied to determine the characteristics of the actual seasonal kill so that errors of the survey estimates could be investigated. Primary emphasis was given to ducks bagged because large samples were obtained on each study area as contrasted to other classes of waterfowl which were not in large numbers on all areas. Data presented are on ducks bagged, unless otherwise identified.

An important relationship on which detailed information was necessary was the seasonal bag frequency. Examination of the distributions revealed several relationships and characteristics which led to recognition and a better understanding of the mail survey errors.

It was concluded that the following char-

acteristics are common to all seasonal waterfowl kill frequency distributions:

1. The relation between seasonal bag frequency and distribution of the hunters is a progressive one, consistently changing throughout the frequency range, rather than fluctuating back and forth.

2. An increase in the seasonal bag frequency size is associated with a decrease in the hunter-occurrence, with one exception (an increase from; the size frequency one less than, to that equal to, the daily bag limit).

3. The maximum proportion of hunter occurrence is found with the lowest seasonal bag frequency size (0) and the minimum proportion of hunter occurrence is found with the largest seasonal bag frequency. These three characteristics will always place the following four limitations on the shape of the frequency distributions: (a) The curve changes shape continuously and progressively, with only one point of inflection which coincides with the daily bag limit. (b) The curve has no positive slope throughout its entire length, except at the frequency size of one less than, to that equal to, the daily bag limit. (c) The minimum number of hunters (one) is reached at the end of the curve and the maximum number of hunters occurs at the beginning of the curve. (d) The curve ends with a long tail which results from the right skewed distribution becoming discontinuous.

These four limitations are apparent in the curves yet they exclude other types of curves from being accepted as indicating the true relation between hunters and seasonal bag of ducks (Fig. 1).

In addition to determining the general limitation relative to skewness listed in (d) above, the skewness was measured for each of the distributions to determine departure from symmetry, where skewness is zero. The distribution of the seasonal duck bag from Lower Klamath Public Hunting Area following the 1951 season showed a skewness of $-.49$ while the Bear River Public Hunting Area distribution had a skewness value of $-.56$. The probability for obtaining such skewness by chance was found to be .25 P. and .08 P. Distributions obtained during the 1952 hunting season on these and the two new study areas were similarly right skewed. The variance of the distributions was found to be larger than the means and

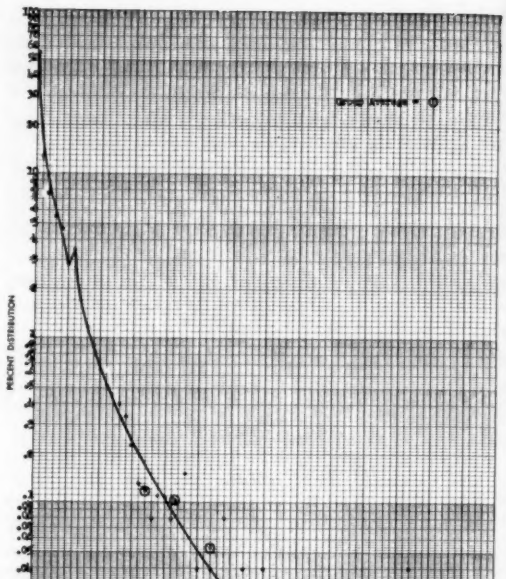

FIG. 1. Actual kill data from Lower Klamath Public Hunting Area, 1951.

in all cases chi-square tests indicated the probability of agreement with the Poisson series was less than .001. As a result of the above tests and the fact that the distributions contained a single mode they were considered to be negative binomials.

VALIDITY OF SURVEY DATA

In a report on response errors in Census Research, Marks and Mauldin (1950) after making suggestions relative to the pitfalls of *a priori* assumptions about a survey method made the following statement: "We cannot overstress the need for empirical test of assumptions. This does not mean we would advocate purely empirical methods. If improvements in techniques are to be made, we must combine a sound theoretical formulation with rigorous empirical tests." These recommendations were followed in determining validity of mail survey data on waterfowl hunting kill occurring on the study areas. Emphasis was given to empirical methods.

Two potential survey errors, which have their origin in sampling, were eliminated in

the survey design. The bias arising from failure to randomize the starting point of a systematic selection was eliminated by sending questionnaires to all hunters which also eliminated any possibility of bias error due to judgment selection of a sample.

Other errors which cannot be eliminated by survey design were identified and measured in our empirical tests. The total net survey error was determined for the responses from the first, second, and third mail contacts. It was also determined for the errors in original plus responses from second contact and for original plus second and third contact responses. The total net error of these responses was determined by comparing means of responses with the true mean, determined from the total of hunters and seasonal bag for each study area (Tables 2 and 3). The smallest error did not occur when the largest number of responses were used to determine the mean. An explanation of this phenomenon was obtained after analysis of several errors which are included in the total net error.

The survey sampling error was determined by comparing the estimate of total ducks bagged, obtained by expansion of the sample of true number of ducks bagged by the survey respondents, with the actual total ducks bagged. In other words, the true number of ducks bagged by the respondents from each mail contact was used as a separate sample for estimating total ducks bagged. The sampling error was the difference between the estimate so obtained and the known total kill. By this method it was possible to determine the sign of the error in addition to its size.

The compensating effect of errors of unlike sign to reduce the net sampling error, when the sample data of responses from waves of successive contacts are pooled, is illustrated in the ducks series from the Bear River area and the goose series from the Lower Klamath area which contain both positive and negative sampling errors (Table 4).

NON-RESPONSE ERRORS—Statisticians have advanced the generally accepted thesis that the characteristics of the respondent population usually differ from the non-respondent population. However, the data from successive waves of requests have usually exhibited differences which have been attributed to differences in the characteristics of the successive response segments of the population and therefore, by deduction, it has been concluded that the characteristics of the non-response segments likewise differ from the response segments. If non-response errors were present in our data the above thesis would be verified with respect to mail surveys of waterfowl kill. If the non-respondent population in our survey differed from the respondent population of hunters the difference would be reflected as an error in the calculated mean ducks bagged by the respondent population. However, only sampling error and non-response error could occur in the mean of the samples of the true kill data of the respondents, whereas many other errors occur in the reported kill. Since true kill data were available for the respondents an analysis of the error occurring in them was carried out as follows. As with the sampling error measurement, the actual kill of the respondents replying to the different mail contacts and the non-respondents were assumed to be separate samples of the hunters using the respective study area. The general hypothesis was then made

TABLE 2.—TOTAL SURVEY ERRORS—DUCKS

Study Area	Hunting Season	Survey responses from contact nos.	Net errors, in per cent of true mean	No. of responses
Lower Klamath, Calif.	1951–52	1	127.73	923
		2	104.15	426
		3	142.32	238
		1+2	119.40	1349
		1+2+3	126.68	1587
	1952–53	1	167.24	973
		2	149.24	535
		1+2	160.85	1508
Bear River, Utah	1951–52	1	33.05	947
		2	16.16	338
		3	37.14	149
		1+2	22.05	1285
		1+2+3	26.05	1434
	1952–53	1	107.39	777
		2	103.55	466
		1+2	105.91	1243
Fountain Grove, Mo.	1952–53	1	52.76	562
		2	58.37	436
		1+2	55.21	998
Trimble, Mo.	1952–53	1	89.00	404
		2	110.56	263
		1+2	102.02	667

TABLE 3.—TOTAL SURVEY ERRORS—GEESE AND COOTS

Study Area	Waterfowl	Hunting Season	Survey Responses from contact numbers	Net errors, in per cent of true mean	No. of responses
Lower Klamath, Calif.	Geese	1951–52	1	140.20	923
	"		2	152.00	426
	"		3	137.26	238
Bear River, Utah	"	1951–52	1	292.00	947
	"		2	356.46	338
	"		3	320.66	149
Lower Klamath, Calif.	"	1952–53	1	245.16	973
	"		2	274.53	535
Bear River, Utah	"	1952–53	1	186.90	777
	"		2	153.40	466
Fountain Grove, Mo.	"	1952–53	1	249.25	562
	"		2	601.80	436
Lower Klamath, Calif.	Coots	1951–52	1	1070.50	923
	"		2	784.70	426
	"		3	1694.60	238
	"	1952–53	1	940.80	973
	"		2	287.90	535
Bear River, Utah	"	1952–53	1	2000.70	777
	"		2	3549.00	466
Fountain Grove, Mo.	"	1952–53	1	187.50	562
	"		2	436.50	436
Trimble, Mo.	"	1952–53	1	58.84	404
	"		2	99.75	263

that the samples were unbiased and from the same population. Statistical test verified the hypothesis that all of the means from each series were from the same populations.[1] The tests also showed that all of the differences between the sample means and the true mean were the result of sampling errors. It was concluded that the characteristics of the non-respondent population of hunters and respondent population of hunters are similar in mail surveys, and that differences exhibited in data from successive waves of requests must be attributed to errors other than non-response errors.

VOLUNTARY AND INVOLUNTARY RESPONSE ERRORS—Since the remainder between the total error, as determined in this investigation, and sampling error contains that portion of error attributable to all biases and since we have demonstrated that non-response error did not occur among our survey errors the remaining survey error can be attributed to response errors.

[1] t tests after group comparisons with different numbers of individuals, transformed to logarithms, yielded values with $P > .50$.

TABLE 4.—SAMPLING ERRORS—1951 SERIES

Study Area	Waterfowl Bagged	Responses from contact number:	Sampling error in per cent	Size of sample
Lower Klamath Public Hunting Area:	Ducks	1	−1.36	923
	"	2	−7.54	426
	"	3	1.90	238
	"	1 & 2	−3.31	1349
	"	1+2 & 3	−2.53	1587
	Geese	1	.40	923
	"	2	−7.54	426
	"	3	7.81	238
	"	1 & 2	−2.52	1349
	"	1+2 & 3	.98	1587
Bear River Public Hunting Area:	Ducks	1	4.48	947
	"	2	−12.67	338
	"	3	−1.51	149
	"	1 & 2	.03	1285
	"	1+2 & 3	.18	1434

The method followed in determining these errors of the mail survey, consisted in comparing the distribution of hunters in frequency classes of ducks actually bagged dur-

ing the hunting season with the distribution of hunters in the frequency classes of the questionnaire reported ducks bagged during the hunting season. Survey response errors results from a distorted distribution of hunters within the frequency classes of seasonal ducks bagged. The effects of the distortions in the survey data will be considered in detail. Response errors are the result of respondent's mental factors and are not removed or diminished by increasing the size of the sample.

Prestige-bias was among the three different voluntary and involuntary response errors identified in our survey data. This error arises from pride (Deming, 1950); the respondents upgrade their actual hunting success with respect to the number of daily bag limits included in questionnaire reports of their seasonal waterfowl bag. A comparison, by class frequencies, of the true seasonal kill on the study areas with the reported kill reveals a definite pattern of survey error which may occur in all multiples of the daily bag limit. The pattern of this positive error is shown graphically in Figure 2.

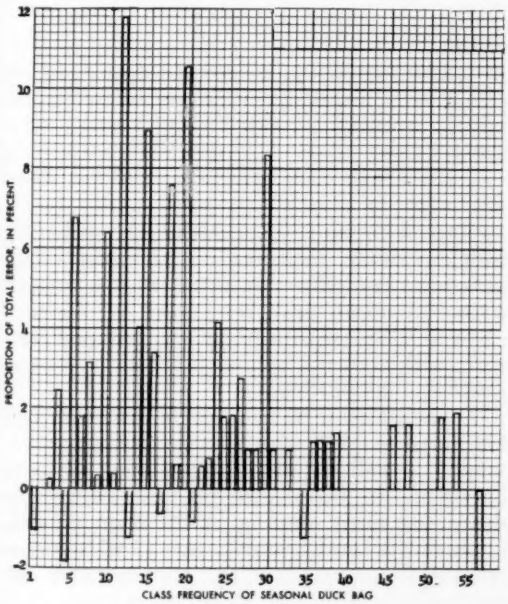

FIG. 2. Lower Klamath Area errors in combined responses from first and second contacts, 1951–52 season.

Smith (1935) used track records of 1,000 high school students to check statements they made about their records in a questionnaire. He concluded that questions involving judgment and personal data obtain responses colored by a constant error of overstatement. Stoke and Lehman (1930) found that seven out of eight students overestimated the number of library books they had borrowed from the library reserve desk for assigned work. The best students exaggerated least and the poorer students most.

Statistical tests on 28 sets of data obtained in the investigation on ducks, geese and coots bagged, revealed that a significant correlation coefficient, $r = .87$, occurred between the ratio of the number of multiples of the daily bag limit occurring in the distribution of hunter responses to the range of this distribution *vs.* the prestige-bias errors occurring in the distribution. The coefficient of determination, shows that about 76 per cent of the variance in the prestige-bias error could be accounted for by differences in the ratio of the number of multiples of the daily bag limit to the range of the distribution of hunter responses in which they occurred. Since this leaves only 24 per cent of the variance to be accounted for by all other factors, it would appear that daily bag limit was the most important factor associated with prestige-bias error. The fact that 76 per cent of the variance in this error can be explained by corresponding differences in the ratio of the number of multiples of the daily bag limit to the range of the distribution of hunter responses in which they occur does not mean that these differences caused the differences in prestige-bias error, but it does show the way in which they are related. We interpret this relationship to support the hypothesis that the cause of the prestige-bias error is associated with the phenomena of pride or prestige of the hunter respondents (Table 3a).

The expression [2] obtained for the above relationship was $Y = -8.9 + 5X \pm 37.8$. When the daily bag is larger than the range of the hunter response distribution for certain waterfowl, no prestige-bias error occurs. It is evident from the above expression that when bag limits are small and the range of the distribution is large the resulting pres-

[2] Where X is the ratio, in per cent, of the number of multiples of the daily bag limit occurring in the distribution of hunters responses to the range of this distribution.

TABLE 3A.—PER CENT OF PRESTIGE-BIAS ERROR VS. MULTIPLES OF THE DAILY BAG LIMIT OCCURRING IN RESPONDENT REPORTED SEASONAL BAG DISTRIBUTIONS

Season	Study Area	Res. No.	Waterfowl Kind	Distribution range	Mult. of bag limit in distribution	Col. 6/ Col. 5, in %	% Prestige bias error
1.	2.	3.	4.	5.	6.	7.	8.
1951	L. Klamath	1	ducks	0 - 87	6	6.9	50.5
1951	L. Klamath	2	ducks	0 - 36	6	16.7	35.0
1951	L. Klamath	3	ducks	0 - 47	4	8.5	31.8
1951	B. River	1	ducks	0 - 80	8	10.0	13.0
1951	B. River	2	ducks	0 - 78	7	9.0	7.1
1951	B. River	3	ducks	0 - 97	5	5.1	2.9
1952	L. Klamath	1	ducks	0 - 119	16	13.4	64.6
1952	L. Klamath	2	ducks	0 - 180	14	7.8	64.4
1952	L. Klamath	1	geese	0 - 37	13	35.1	153.2
1952	L. Klamath	2	geese	0 - 70	16	22.9	189.4
1952	L. Klamath	1	coot	0 - 35	2	5.7	77.5
1952	L. Klamath	2	coot	0 - 16	0	0	0
1952	B. River	1	ducks	0 - 200	15	7.5	35.6
1952	B. River	2	ducks	0 - 101	14	13.9	28.6
1952	B. River	1	geese	0 - 13	2	15.4	68.0
1952	B. River	2	geese	0 - 16	3	18.7	84.2
1952	B. River	1	coot	0 - 3	0	0	0
1952	B. River	2	coot	0 - 6	0	0	0
1952	F. Grove	1	ducks	0 - 38	5	13.1	23.1
1952	F. Grove	2	ducks	0 - 40	7	17.5	12.4
1952	F. Grove	1	geese	0 - 3	1	33.3	163.6
1952	F. Grove	2	geese	0 - 6	3	50.0	348.6
1952	F. Grove	1	coots	0 - 3	0	0	0
1952	F. Grove	2	coots	0 - 6	0	0	0
1952	Trimble	1	ducks	0 - 20	4	20.0	22.6
1952	Trimble	2	ducks	0 - 27	2	7.4	6.8
1952	Trimble	1	coots	0 - 11	0	0	0
1952	Trimble	2	coots	0 - 10	1	10.0	11.1

tige-bias error is very large. The former situation sometimes occurs with coots, where daily bag limits of up to 25 have occurred in recent years, while the latter situation usually occurs with geese where bag limits of 2 are common. A range of 0–349 per cent bias error occurred among the 28 sets of data obtained.

Analysis of the proportion of first contact responses containing larger prestige-bias errors as compared to second contact responses prestige-bias errors did not reveal significant differences in the pooled sample containing data for ducks, geese and coots, or when coots and geese data were tested as separate groups. However, when data for ducks were tested as a group, the proportion of first *vs.* second prestige-bias response errors was so large that the probability of obtaining it by chance combinations was only 3 in 100.

Type I memory-bias, although operating independently, is closely associated with prestige-bias. Like the latter, it stems from over-statement and results in a positive error and occurs in a fairly well-defined pattern, although not as sharply defined as the prestige-bias pattern.

A comparison of the actual seasonal bag size classes with the survey responses revealed a well defined exaggeration pattern occurring in those size classes, above the daily bag limit, ending in the digit 0 or 5, (Figure 3). Linder and Grove (1947) in discussing inaccuracies in the statement of age on death certificates attribute a large part to errors in the statement of age. They reported that these errors result in a characteristic excess of deaths at reported ages ending in the digit 0 or 5. The same kind of error occurs in the age data obtained during the decennial census, with an additional bias

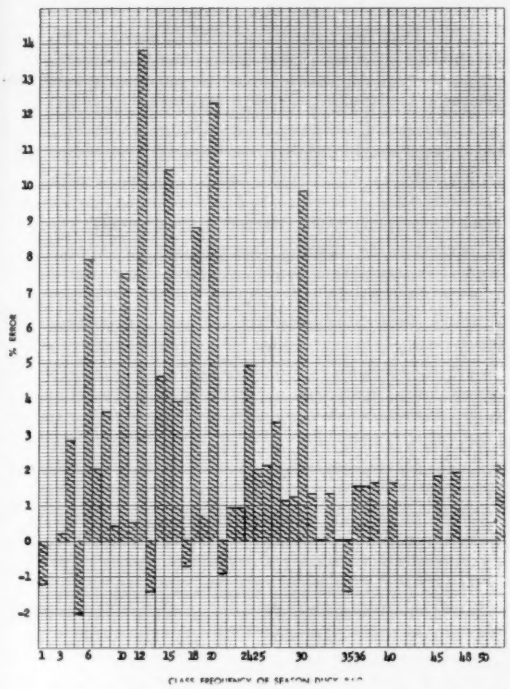

FIG. 3. Questionnaire data errors; Lower Klamath Area.

error at age 21. These errors are small as compared to the memory errors in our survey, Table 5, and Table 5a. Deming (1950) attributes memory-bias error to guessing made necessary through lack of records.

Statistical tests on 28 sets of data obtained in the investigation, on ducks, geese and coots bagged, revealed that a highly significant correlation coefficient, r = .65, occurred between the ratio of the number of digits divisible by 5 occurring in the distribution of hunter responses to the range of this distribution *vs.* the Type I memory-bias error occurring in the distribution. The coefficient of determination shows that only about 42 per cent of the variance in this Type I memory-bias could be accounted for by differences in the ratio of the number of digits divisible by 5, occurring in the distribution of hunter responses, to the range of these responses. We interpret this relationship to indicate that about 40 per cent of the cause of Type I memory-bias is associated with guessing made necessary through lack of records. We suspect that most of the remaining cause should be associated with the phenomena of pride or prestige of the hunter respondents. A range of 0–418 per cent Type I memory-bias error occurred among the 28 sets of data obtained in the study.

In our comparison of the true seasonal bag frequencies with the frequencies of the survey responses another type of exaggeration error was revealed, we named it Type II memory-bias. In contrast to the regular pattern of error in the digits ending in 0 and 5, the pattern of occurrence was irregular and therefore less obvious. This error occurs in one or all of the following three forms in the survey responses: 1. The length of the survey response distribution of seasonal bag frequencies exceeds the distribution of true bag frequencies. 2. The total number of frequency classes in the survey response distribution exceeds the total number of classes in the true bag distribution. 3. As

TABLE 5.—SUMMARY OF MAIL SURVEY ERRORS, BY STUDY AREAS, FOR 1951–52 RETRIEVED DUCKS

Study Area	Response number	Prestige-bias error in per cent	Detected Type I memory-bias error in per cent	Estimated Type II memory-bias error in per cent	Estimated total memory-bias error in per cent	Sampling error in per cent	Total gross error in per cent	Total Net error in per cent
Lower Klamath Public Hunting Area	1	50.47	35.09	43.53	78.62	−1.36	129.09	127.73
	2	35.05	42.90	33.74	76.64	−7.54	111.69	104.15
	3	31.79	33.46	75.17	108.63	+1.90	142.32	142.32
Bear River Public Hunting Area	1	13.02	12.09	3.46	15.55	4.48	33.05	33.05
	2	7.14	12.81	8.88	21.69	−12.67	28.83	16.16
	3	2.91	33.51	2.23	35.74	−1.51	38.65	37.14

TABLE 5A.—SUMMARY OF MAIL SURVEY ERRORS, BY STUDY AREAS, FOR 1952–53 RETRIEVED DUCKS

Study Area	Lower Klamath Public Hunting Area		Bear River Public Hunting Area		Fountain Grove Public Hunting Area		Trimble Public Hunting Area	
Sample response from mail contact number:	1	2	1	2	1	2	1	2
Total net error, in per cent	167.60	148.84	108.59	103.83	53.02	58.98	89.12	121.75
Total gross error, in per cent	167.60	153.11	108.59	108.42	56.33	58.98	94.86	121.75
Calculated sampling .50P	+2.87	−4.27	+3.30	−4.59	−3.31	+3.98	−5.74	+7.82
error, in per cent .95P	8.35	−12.41	+9.58	−13.34	−9.60	+11.54	+16.68	22.72
Estimated total memory-bias error, in per cent	100.27 or 106.01	81.02 or 89.56	73.16 or 79.76	70.67 or 79.85	26.61 or 33.23	42.63 or 50.59	60.78 or 72.26	108.91 or 124.55
Estimated Type II memory-bias error, in per cent	48.66 or 54.40	8.99 or 17.53	29.17 or 35.77	19.10 or 28.28	21.77 or 28.39	21.37 or 29.33	44.05 or 55.53	67.35 or 82.99
Detected Type I memory-bias error, in per cent	51.61	72.03	43.99	51.57	4.84	21.26	16.73	41.56
Prestige-bias error, in per cent	64.63	64.63	32.70	28.57	23.10	12.37	22.59	6.83

compared to the actual frequency distribution of the hunters by bag size, the frequency of occurrence of hunters in the survey responses is slightly too low in the first few and too large in the remaining size classes. In the survey responses the percentage of error increases as the seasonal kill increases.

The pattern of occurrence and the positive nature of these errors is apparent when the distribution of hunters reported by questionnaire in Column 3 of Table 6 is compared to the actual distribution of hunters in Column 2.

An elaboration of each of the above forms of this so-called second type of memory-bias exaggeration appears desirable. In a previous section on characteristics of the true data on waterfowl bagged, one of the statements of curve characteristics stated that the curve ends with a long tail which results from the distribution becoming discontinuous. It is in this portion of the curve that most of the errors of this second type of memory-bias occur. The explanation for this phenomenon is as follows: The tail portion of the distribution begins with the first break in the continuous series of whole digits. Therefore, the excess in number of frequency classes in the survey response distribution must occur in this tail portion of the distribution, because up to this first break every possible size class occurs in the true distribution. The excessive length of the survey response distribution must likewise occur at the extreme end of the tail, because the length of the distribution is defined as the difference between the maximum and minimum seasonal bag size.

In the third form of this second type of memory-bias exaggeration, the error increases as the seasonal bag classes increase in size. Lines fitted to the frequency errors by the method of least squares (excluding the frequencies which were multiples of the daily bag limit and those with digits ending in 0 and 5) revealed that the slope is positive, (Figure 4). This of course indicates that the amount of error increases in the survey responses as the reported seasonal bag size increases. We interpret this trend to further indicate that at any given time after their last hunting trip, in the absence of records, hunters can more reliably recall small seasonal totals (resulting from one or a few

TABLE 6.—COMPARISON OF CORRECTED AND ORIGINAL SURVEY DATA WITH ACTUAL KILL DATA FROM LOWER KLAMATH PUBLIC HUNTING AREA, 1951

Class frequency of bag	Number of hunters: Actual	Questionnaire	Estimated from curve
0	753	567	759.00
1	174	145	145.00
2	102	102	102.00
3	75	77	77.00
4	63	80	60.00
5	38	48	48.00
6	47	79	39.00
7	23	30	30.00
8	12	23	20.00
9	12	13	13.00
10	7	25	9.00
11	7	8	6.60
12	6	34	5.00
13	6	4	4.00
14	4	12	3.30
15	3	20	2.70
16	2	8	2.30
17	2	1	2.00
18	2	14	1.80
19	1	2	1.60
20	1	16	1.50
21	1	0	.00
22	1	2	1.30
23	1	2	1.20
24	0	5	1.10
25	1	3	1.00
26	0	2	1.00
27	1	4	.96
28	0	1	.94
29	1	2	.86
30	0	8	.81
31	0	1	.80
32	1	1	.76
33	0	1	.74
34	0	0	.00
35	1	0	.00
36	0	1	.66
37	0	1	.65
38	0	1	.63
39	0	0	.00
40	0	1	.59
45	0	1	.52
47	0	1	.50
52	0	1	.45
54	0	1	.43
57	1	0	.00
87	0	1	.30
	1349	1349	1349.00

hunting trips) as compared to increasingly larger seasonal totals (resulting from several to numerous hunting trips).

Type II memory-bias error was determined by subtracting the sampling error from the sum of the net error occurring in the survey response seasonal bag size classes as compared to the true bag size distribution, but excluding size classes divisible by 5 and those which were multiples of the daily bag limit.

The factors associated with the above response error are more numerous than those concerned with prestige and Type I memory-bias errors. They are also less obvious and the relationships more complex. Suffice it to say that this error was found to occur in all of the surveys investigated, including geese and coots in addition to ducks bagged. The range of error was approximately from 3 to 400 per cent.

DISCUSSION—The results of the study demonstrate that post-season survey responses from waterfowl hunters always contain response errors originating from pride, prestige and memory failure of the waterfowl hunter in addition to sampling errors. Since the response errors are not consistent as to size from one area to another nor from one year to another on the same area and are large as compared to sampling errors, their presence very seriously limits the usefulness of the survey data.

For example, although there was an actual decrease of 14.3 per cent in the average seasonal duck kill per hunter on the Bear River Public Hunting area during the 1952–53 season as compared to the 1951–52 season, the mail survey data indicated the average seasonal duck bag to have increased 32.0 per cent during the same period. On the Lower Klamath area during the same period the actual average goose bag per hunter decreased by 13.6 per cent, but the mail survey data indicated the kill to have increased by 21.3 per cent. On the other hand, the actual average coot bag per hunter on Lower Klamath increased 2873 per cent, while the survey data indicated the increase to have been 1603 per cent. While the remaining estimates of difference in kill between the 1951–52 and 1952–53 seasons, as determined by use of the survey data, were in the same direction as shown by the actual bag data the minimum discrepancy in the survey data estimate of change was 33.0 per cent. The inconsistency of the expansion factor in the response errors from one area to another is illustrated by the range of the net positive

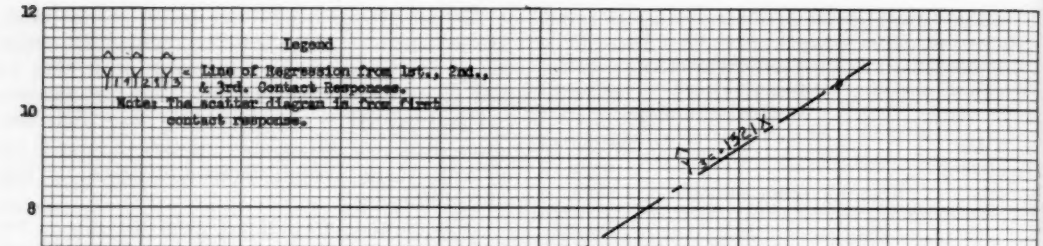
Legend
Lines of Regression from 1st., 2nd., & 3rd. Contact Responses.
Note: The scatter diagram is from first contact response.
% ERROR
CLASS FREQUENCY OF SEASONAL DUCK BAG

FIG. 4. Type II memory bias questionnaire errors; Lower Klamath Area.

errors for all areas and all groups for the two season period, these errors ranged from 16 to 3549 per cent.

It is evident that response errors will always occur in hunter bag data obtained from post-season contacts regardless of whether the contacts were made by mail, phone or personal interviews. Hjersman (1951) reported data obtained from post-season personal interview contacts was comparable to that obtained from mail contacts in California following the 1948 hunting season. Since he suspected an inflation error to be present in both mail and interview data, which our investigation has confirmed, it would appear that the magnitude of response errors in data from post-season personal interview contact of hunters is substantially the same as would occur from the same sample by mail contact.

Since response errors of large magnitude may occur in any sampling plan which includes post-season contacts of hunters for obtaining estimates of hunting take, the reliability of all such estimates is highly suspect. Consequently, before such data can have practical management significance, the effect of most response-bias errors must be removed.

REMOVAL OF RESPONSE BIAS ERRORS

A graphical method of preliminary analysis had indicated the presence of bias errors in seasonal bag classes which were multiples of the daily bag limit and in those size classes divisible by five. This suggested the graphical method as a good possibility for reducing the effect of that portion of response errors occurring in these size classes.

A graphical adjustment was carried out by constructing a freehand curve of the survey data from those frequency classes remaining after eliminating the predictable biased frequency classes referred to above. In order to obtain a greater degree of precision and to insure that the same data would yield substantially the same result even in the hands of different investigators, group averages were used for reference points in constructing the curve, as suggested by Ezekiel (1950). A smooth curve was next developed (Fig. 1) by reference to the plotted

points and consideration of the four limitations to the shape of the curve as developed in the study of the true kill frequency distributions (*op. cit.*). Table 6 shows the true distribution of hunters, the distribution from the combined responses (the first and second contacts) and the estimated distribution as read from the freehand curve constructed from 1951 Lower Klamath survey data.

The graphical approach was found to be satisfactory for adjustment of the bias errors whose pattern of occurrence is predictable; it is not as satisfactory for the Type II memory-bias error because this error may occur in all of the remaining bag size classes not included among those identified with the biases listed above. However, two of the three forms of Type II memory-bias errors occur in the discontinuous portion of the distribution. The per cent of Type II memory-bias error increases as the seasonal bag size increases and the largest bag sizes occur in the tail portion of the distribution. Thus if a valid adjustment could be found to remove the Type II memory-bias error in this discontinuous portion of the distribution only that part would remain which occurs within the continuous portion of the distribution. Some rough tests indicated that from one-third to almost half of this error occurred in the discontinuous portion of the distribution. This was considered of sufficient magnitude to justify further efforts to develop an adjustment for the removal of error in the tail of the survey distribution.

Analysis showed that the degree of skewness varied with the mean season duck bag. The distribution of the total ducks bagged in terms of standard deviations from the mean, was different for areas having different season means. However, analysis in terms of cumulative per cent of total ducks bagged, revealed a general similarity in that portion of the distribution from the mean plus 5 to the mean plus 7 standard deviations in all of the study areas (Table 7). Furthermore, in the region of the beginning of discontinuity of the distribution, which corresponds approximately to the range of the mean plus six standard deviations, the cumulative per cent of total ducks bagged on the four study areas averaged 95.52 per cent, the range of cumulative totals, being from 94.49 per cent to 96.75 per cent. This similarity prevails despite the dissimilarity of the respective seasonal bag range included for the several areas. Since the beginning of the discontinuous portion corresponds approximately with that part of the distribution equivalent to the mean plus six standard deviations, and an average of 95.52 per cent of the total ducks bagged occurs within this range, regardless of the difference in size of the season duck bag mean, it is possible to use this information to advantage in eliminating the effect of the Type II memory-bias errors. It has been shown that 95.52 per cent of the total ducks bagged occurs under the area of the curve corresponding to six standard deviations from the true mean of the seasonal ducks bagged. There-

TABLE 7.—THE RELATION OF CUMULATIVE TOTAL DUCKS BAGGED TO THE ACTUAL DISTRIBUTION OF HUNTERS IN THE FREQUENCY CLASSES OF THE SEASONAL BAG

Distribution of the Hunter Universe as the Mean Plus and Minus Multiples of the Standard Deviation	Cumulative Per cent of Total Ducks Bagged and the Corresponding Seasonal Bag Range								
	Lower Klamath		Bear River		Fountain Grove		Trimble		Mean
	Range	Per cent	Range	Per cent	Range	Per cent	Range	Per cent	Per cent
1.....	0– 5.4	42.78	0–13.3	58.71	0– 5.0	62.32	0– 2.1	39.77	.....
2.....	0– 9.0	69.28	0–21.4	73.08	0– 7.6	80.42	0– 3.5	56.27	.....
3.....	0–12.6	78.45	0–29.3	80.46	0–10.3	86.58	0– 5.0	78.70	.....
4.....	0–16.2	86.48	0–37.4	87.61	0–12.9	91.80	0– 6.4	82.93	.....
5.....	0–19.8	89.65	0–45.4	92.47	0–15.6	95.33	0– 7.8	95.48	93.25
6.....	0–23.3	94.89	0–53.4	94.49	0–18.3	95.96	0– 9.3	96.75	95.52
7.....	0–26.9	96.44	0–61.4	97.71	0–20.9	97.82	0–10.7	98.16	97.28
8.....	0–30.5	97.31	0–69.4	98.72	0–23.6	98.63	0–12.1	99.94	.....
9.....	0–34.1	98.01	0–77.4	98.72	0–26.2	.....	.....	.....	.....
10.....	0–37.7	98.78	0–85.5	99.37	0–28.9	.....	.....	.....	.....

fore, the survey sample estimate of ducks bagged under the area of the graphically adjusted curve corresponding to six standard deviations from the corrected mean is an estimate of 95.52 per cent of the ducks bagged. Then the quotient of the above sample estimate and .9552 is an estimate of 100 per cent of the ducks bagged. This last estimate eliminates the effect of the response-bias errors occurring in the response survey distribution beyond six standard deviations from the mean.

It was also found that 95.49 per cent of the total geese bagged occurs under the area of the curve corresponding to six standard deviations from the true mean of the seasonal geese bagged (Table 8). However, the range of cumulative totals at six standard deviations was larger than at four, i.e., 88.56–99.70 per cent *vs.* 88.56–93.48 per cent. Use of the .9549 factor to correct for response-bias errors occurring in the survey distribution beyond six standard deviations from the mean would introduce a negative error of about eight per cent in distributions where the range was no greater than five and introduce a positive error of about four per cent where the range is ten or more. However, if the factor .9127 is used with the cumulative total occurring at the range of four standard deviations from the corrected mean, the negative error introduced in distributions of low range and positive errors introduced in distributions of large range would both be about two per cent and therefore largely compensating where stratified sampling is used.

EFFICIENCY OF ADJUSTMENTS OF SURVEY DATA—The efficiency of the two techniques described for reducing the response-bias errors in sample data from hunter questionnaire responses is high. This situation holds when the total bias-errors are only moderately great as well as when these errors are very great.

An example of their application to two wave request responses from hunters using the Lower Klamath and Bear River areas during the 1951–52 season will illustrate the efficiency on data in this category. The original and subsequent remaining errors were determined by comparison of the survey data with the true bag data for each study area. The distribution of total error for this series on the Lower Klamath area is shown on Fig. 2. The pattern of the preponderantly positive response biases is clearly shown. The range corresponding to six standard deviations from the graphically adjusted sample mean is 0 through 30. The positive Type II memory-bias errors are evident beyond frequency 30 as well as prestige-bias errors at frequencies 36 and 48 which are multiples of the daily bag limit of six. Table 9 shows the errors occurring be-

TABLE 8.—THE RELATION OF CUMULATIVE TOTAL GEESE BAGGED TO THE ACTUAL DISTRIBUTION OF HUNTERS IN THE FREQUENCY CLASSES OF THE SEASONAL BAG

Distribution of the Hunter Universe as the Mean Plus and Minus Multiples of the Standard Deviation	Cumulative Per cent of Total Geese Bagged and the Corresponding Seasonal Bag Range						
	Lower Klamath 1951–52		Lower Klamath 1952–53		Bear River 1952–53		Mean
	Range	Per cent	Range	Per cent	Range	Per cent	Per cent
1.....	0– 2.5	60.76	0– 2.1	52.04	0– .5	0	.....
2.....	0– 4.1	73.74	0– 3.4	67.73	0–0.8	56.58	.....
3.....	0– 5.6	86.68	0– 4.8	89.77	0–1.2	56.58	.....
4.....	0– 7.2	91.76	0– 6.1	93.48	0–1.6	88.56	91.27
5.....	0– 8.8	95.65	0– 7.4	96.66	0–1.9	88.56	93.62
6.....	0–10.4	98.21	0– 8.8	99.70	0–2.3	88.56	95.49
7.....	0–11.9	98.68	0–10.1	99.70	0–2.7	94.71	.....
8.....	0–13.5	99.28	0–11.4	100.00	0–3.1	94.71	.....
9.....	0–15.1	100.00	.....	.....	0–3.4	94.71	.....
10.....	.....	.....	.....	.....	0–3.8	97.99	.....
11.....	.....	.....	.....	.....	0–4.2	97.99	.....
12.....	.....	.....	.....	.....	0–4.5	100.00	.....

TABLE 9.—EXAMPLE OF EFFICIENCY OF METHODOLOGY OF ADJUSTMENT OF QUESTIONNAIRE DATA

Study Area	Net error of uncorrected survey data	Error of mean after correction for prestige, superstition and Type 1 memory-bias	Error of mean after correction for Type 2 memory-bias	Actual sampling error of respondents duck bag
Lower Klamath.....	116.18%	10.47%	4.05%	−3.31%
Bear River.....	29.02%	−9.42%	−6.95%	0.03%

fore and after the two corrections for response-bias errors were carried out.

The per cent of error remaining after the completion of graphical adjustment was found to be of about the same magnitude, 10.47 for the Lower Klamath area data and −9.42 per cent for the Bear River area data despite the varying differences in the per cent of error in the raw survey data from these areas. Distortions resulting from prestige and Type I memory-bias, no matter how serious, have been eliminated from the curve and therefore errors remaining consist of Type II memory-bias, sampling errors and the possibility of errors introduced by the graphical adjustment. The −9.42 per cent error in the Bear River data mean must be interpreted as showing that a negative error was introduced in the graphical adjustment because the net sum of the response-biases in this data always has a positive sign. This over-correction resulted from failure to provide for a point of inflection at the daily bag limit on the curve of the corrected survey sample to correspond to that which occurred with the true frequency.

The total error remaining in the graphically corrected Lower Klamath mean was reduced by 46.6 per cent and that of the Bear River graphically corrected mean reduced by 26.1 per cent by carrying out the technique for reducing the errors in the tail portion of the survey distribution. The algebraic sum of the errors of the mean and the sampling error is a measure of the error remaining other than sampling error. We find this to be about 7.0 per cent of the true mean for each study area.

DISCUSSION—After the two corrections for response error have been completed, an estimate of the maximum error of the mean, carried out by usual statistical methods, will have meaning in the literal sense. This is true because statistical tests of the error of the mean are only estimates of the sampling error—they are not estimates of the total error when the total includes bias errors. This fact has been passed over lightly or entirely omitted in presentations of data from many polls and surveys with the result that a false sense of reliability has been drawn from the estimates of errors included. This situation occurs because there are no standard methods available for estimating bias errors. The revelation that response-bias errors are relatively large as compared to sampling errors has shown that their occurrence can no longer be ignored in post-season hunter surveys.

Estimates of the maximum error of the mean in examples from the survey investigation shown in Table 4 were carried out after the two corrections for response errors were completed. These estimates were ±7.27 per cent for Lower Klamath and ±5.36 per cent for Bear River at .95 probability. It will be noted that there is good agreement with the true error of the mean after the corrections for response error were carried out, i.e., 4.05 per cent for Lower Klamath and −6.95 per cent for Bear River areas. We would expect the estimate of probable maximum per cent error to exceed the actual error of the mean in 19 out of 20 cases, as in that from the example from the Lower Klamath area. In one out of 20 cases the estimate would be exceeded, as in the example from the Bear River area.

SUMMARY

Knowledge of the pattern of occurrence and characteristics of response errors obtained during an investigation of the validity of post-season surveys of hunters was used to advantage to devise a two-step method for removing the response-bias errors from the raw survey data. The method was tested on data with known errors and found to have a high efficiency in reducing the effect of response-bias errors. The development of this method for removing the effect of the response-bias errors, and its application to

post-season hunter-take survey data, increased the reliability of the data from below the point of practical management significance up to the approximate reliability limits corresponding to the sampling errors.

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NESTING STUDY OF WOOD DUCKS

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Shortly after moving into a new home along the Mississippi River just north of Minneapolis, I became aware of several pairs of wood ducks nesting in hollow basswood trees on the nearby river banks. This extreme accessibility of the birds induced me to begin a study of certain phases of the nesting activities of the birds. A nest box was accepted by them in 1947. Later this box was reconstructed with a "floating" floor and an alarm clock-cake pan recording apparatus as shown in Figure 1. This mechanized box was occupied by a wood duck, possibly the same female, for the three succeeding seasons, 1948, 1949, and 1950. She was not banded during the earlier part of the work since it was feared she would be seriously disturbed or might even desert her nest as a result, and the recording of nesting data seemed more important than the banding of the bird. She was finally banded just before the young left the nest during the spring of 1950.

At first only the nesting rhythm or periods of nest attentiveness were recorded and studied. Later some thermocouple temperature readings were taken as a check on the effectiveness of the down

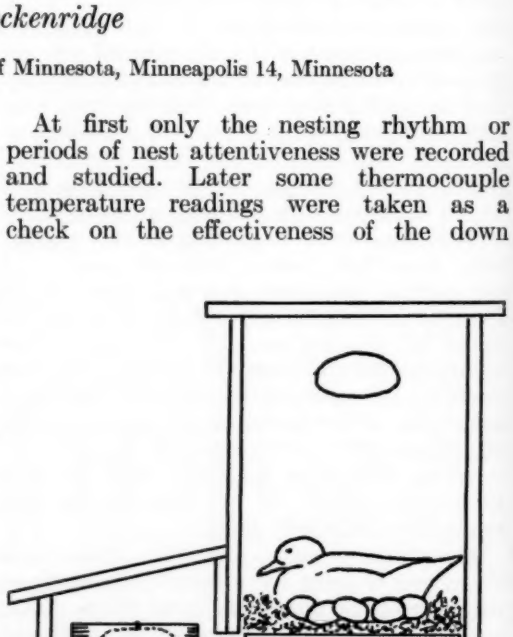

FIG. 1. Floating floor and recording apparatus used in wood duck study.

blanket in retaining the heat in the nest. These data were then utilized in an inquiry into the incubation period of the wood duck.

EGG LAYING—The regularity of early morning egg laying of the bird was noted early in study. The recording apparatus was not perfected in time to secure laying records in 1948 and mechanical difficulties interfered with securing 1950 records. Figure 3 includes the record for the laying period in 1949. The record began with the laying of the third egg on April 17 and shows with what regularity the next eight eggs were laid between 5:00 and 8:00 each morning. Periods on the nest during the laying of eggs varied from 8 minutes to 3 hours and 11 minutes, the average being 1 hour and 48 minutes. Girard (1941) reported female mallards spending an hour to an hour and a half on the nest during the laying of each egg. Although incubation did not start in earnest until the last or 13th egg was laid on April 27, it is significant to note that on April 24 she returned to the nest at 7:11 p.m. and remained there all that night and for the succeeding two nights, the periods during which the last three eggs were being laid. The minimum temperatures for these three nights were not extremely low (46° to 48° F.).

NEST ATTENTIVENESS—Nest attentiveness by the female during incubation was recorded, with only a few minor interruptions due to mechanical failures, for all three seasons 1948, 1949, and 1950. Rather surprising variation appears in these records. The 1950 record (Figure 4) shows an almost perfect pattern of a single feeding period of varying length each afternoon between 5:00 and 8:00. The 1949 record, (Figure 3), on the other hand, shows the usual pattern of two daily feeding periods, one in the morning and one in the afternoon. In 1948 (Figure 2) little or no regularity is discernible. Obviously this activity varies considerably with individuals of the same species and possibly with the same individual in different years. Stoddard (1931) stated that incubating bobwhite normally leave the nest only once each 24-hour period while Girard (1941) found mallards rather typically leaving twice each day. Many workers (Nice, 1943) have recorded on and off periods for smaller song birds and found them varying greatly from 5 to

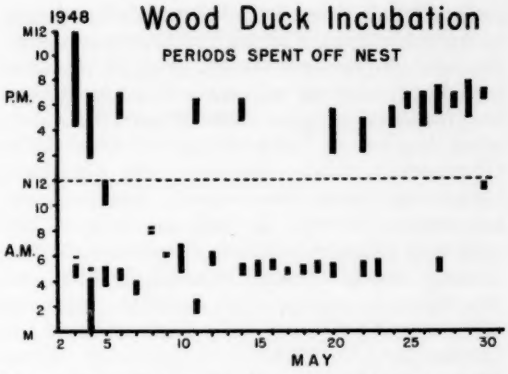

FIG. 2. Recorded incubation of wood duck, 1948.

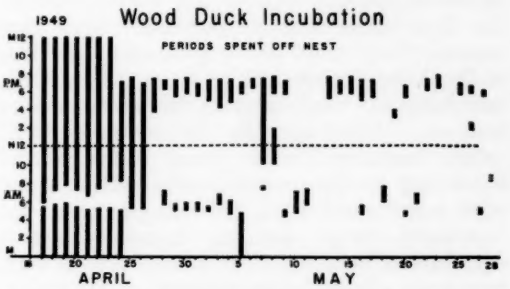

FIG. 3. Recorded egg-laying and incubation of wood duck, 1949.

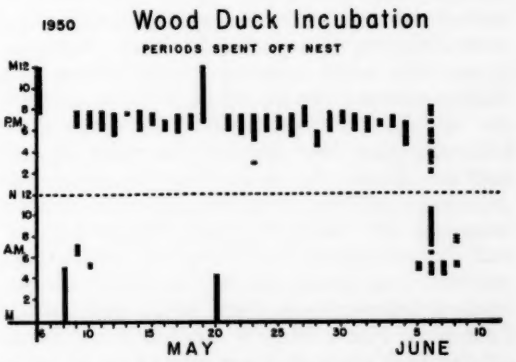

FIG. 4. Recorded incubation of wood duck, 1950.

90 times during a single day. On the other hand, petrels, fulmars, albatross, and penguins are reported as remaining on the nest for several days at a time. Richdale (1942) reported a royal albatross remaining uninterruptedly on the eggs for 14 days.

Nest attentiveness in terms of total time spent off the nest in each 24-hour period was correlated with minimum daily temper-

atures. In all three years' records a tendency to incubate longer on cooler days is evident. Periods off the nest varied from 13 minutes to 4 hours and 40 minutes. The correlation was quite striking in 1948 (Figure 5), somewhat less so in 1949 (Figure 6) and 1950 (Figure 7). This tendency to incubate longer on cooler days seems definitely an adjustment to suit the requirements of the eggs and appears to have no relation to the feeding needs of the incubating birds as has been suggested for certain passerine birds by Kluijver *et al.*, and restated as follows by Nice (1943): "In a study of the European Wren in Holland, females were found on the nest [by observers] 54 percent of the times [the nests were] visited during the first brood and 80 percent during the second: [the suggested explanation of this is that] the female has to spend more time searching for food early in the season than later. . ." Perhaps the larger birds with greater reserve of body energy can incubate according to the requirements of the eggs with less regard to their feeding needs.

Several very definite breaks in the correlation between nest attentiveness and minimum daily temperatures merit some comments since these disturbances enter significantly into the consideration of the incubation period later. No serious disturbances occurred to interrupt incubation in 1948 (Figures 2 and 5). In 1949 (Figures 3 and 6), some unknown disturbance on May 5 sent the female off at 12:07 a.m. and she did not return until 4:50 a.m. The following day her rhythm was still upset and she did not leave the nest at all in the morning and for only 56 minutes in the evening. The following day, May 7, she still did not settle into her usual incubating pattern but remained off in spite of its being relatively cool from 10:11 a.m. until 7:36 p.m. From May 9 on, her total time off the nest each day again became normal and correlated with minimum daily temperatures (Figure 6). In the 1950 record (Figures 4 and 7), mechanical difficulties necessitated extensive repairs to the apparatus at the beginning of the incubation period and the female remained off all night on May 7-8, the third day of incubation, but immediately resumed a normal incubation pattern on May 9. Again on the night of May 19-20 some abnormal circumstance caused her to remain off the nest from 6:41 p.m. until 4:19 a.m., or 9 hours and 38 minutes. Again a normal

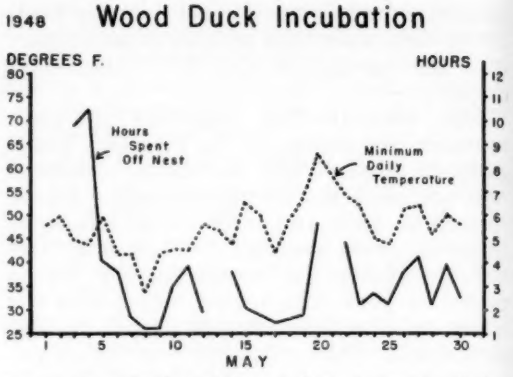

FIG. 5. Recorded periods wood duck spent off the nest correlated with minimum daily temperatures, 1948.

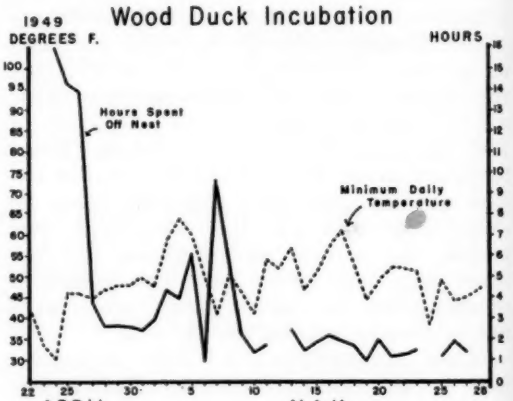

FIG. 6. Recorded periods wood duck spent off the nest correlated with minimum daily temperatures, 1949.

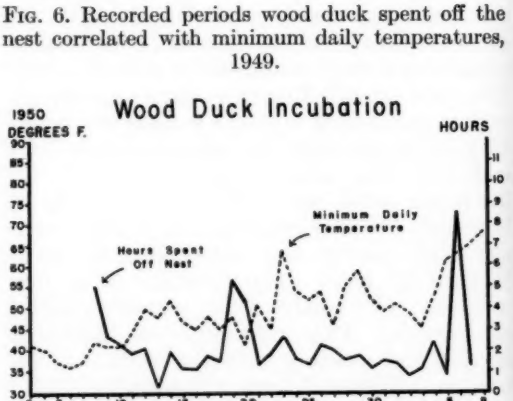

FIG. 7. Recorded periods wood duck spent off the nest correlated with minimum daily temperatures, 1950.

pattern was assumed immediately afterward until June 6, the day the eggs were pipping. The June 6 activities began normally but the bird spent 3 hours and 50 minutes off during the morning and the record shows many short trips away from the nest during the afternoon. When this record was first checked it was thought that these trips were a record of the female removing egg shells from the nest, but a recheck showed that at 6:00 p.m. after most of the trips were over, the eggs were still only pipped so this could not be the explanation. Girard (1941) observed incubating mallards shifting about more on the nest the day the eggs were pipping. The neatly broken half shells from normally hatched eggs were not in the nest after the family left on June 8 and yet no trips away from the nest were recorded on the tape after the young hatched. It is possible that some of these were eaten by the female and/or young but the activity of the adult and young in the nest crushes the shells into tiny bits and they largely disappear into the nest materials.

INCUBATION PERIOD—In 1948 (Figure 5) incubation began on May 5. The young left the nest on May 31, having hatched on the night of the 29th and 30th. Thus the 1948 incubation period was about 25 days. Incubation started in 1949 (Figure 6) on April 27. The young hatched on May 26-27, making the incubation period 29-30 days. In 1950 (Figures 4 and 7) incubation started on May 6 and the young hatched on June 6-7, making the incubation period about 31 days.

Some uncertainty in the above periods results from lack of repeated checking of the eggs and from the fact that all young do not hatch at exactly the same time. However, these factors could hardly account for a 6-day variation in the incubation period of this species. Obviously some factors caused an actual delay in development of the embryos. Some delay has been found by numerous workers to be the result of chilling of the eggs. Landauer (1941) referring to domestic chicken eggs states, "The time of hatch is, of course, delayed by cooling, but, according to Kaufman (1934) the delay is somewhat less than the period of cooling itself."

An examination of the 3-years' wood duck incubation records shows that cooling of the eggs could have been concerned with the varied incubation periods but suggests that the degree and the time of cooling may also be factors in lengthening this period, especially when it is considered that embryos are more resistant to unfavorable conditions during their earlier developmental stages. The 25-day incubation period was recorded in 1948 (Figure 5) when no serious disturbances occurred during incubation. In 1949 (Figure 6) with an incubation period of 29-30 days, the bird was forced off the nest for 2 abnormally long periods on the 9th and 11th days of incubation (May 5 and 8), totaling 14 hours and 8 minutes during which time the outside temperature was rather warm, varying from 61°F. to 76°F. In 1950 (Figure 4) on the third day of incubation the bird was off for 13 hours and 35 minutes when the minimum outside temperature dropped to 42°F. On the 14th day of incubation she was off for 9 hours and 38 minutes when outside temperatures also reached the very low minimum of 41°F. Thus, the most prolonged and severe chilling occurred on the year (1950) when the longest incubation period was recorded (31 days).

It might be thought that the very efficient protection given the eggs by the complete blanket of down present in the nest would prevent any very serious chilling of the eggs even during these prolonged absences of the incubating female. This protection was found not to be as efficient as one might suppose. The detecting terminals of a thermocouple were cast into a plaster of Paris egg and this egg screwed to the bottom of the nest box in the center of the clutch with the contacts lying on the surface of the egg half-way down from the top surface. Thermocouple readings showed the gradual loss of heat at this point among the eggs after the bird had left the nest of its own accord having covered the eggs with down. On one abnormally warm day the outside temperature during the 2 hours and 31 minutes that the duck was absent dropped from about 87°F. to 82.5°F. The heat loss in the nest was only about 7°F. Figure 8 shows the heat loss over a shorter period (1 hour and 22 minutes) but when the much lower outside temperature varied from about 63°F. to 61°F. Under these much cooler conditions the nest temperature dropped about 13.5°F., nearly

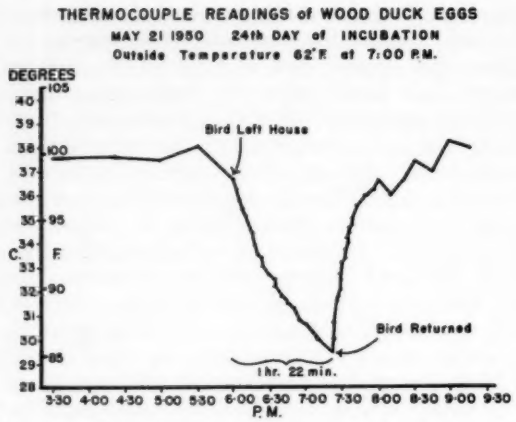
THERMOCOUPLE READINGS of WOOD DUCK EGGS
MAY 21 1950 24th DAY of INCUBATION
Outside Temperature 62°F at 7:00 P.M.
DEGREES
C
F
Bird Left House
Bird Returned
1 hr. 22 min.
3:30 4:00 4:30 5:00 5:30 6:00 6:30 7:00 7:30 8:00 8:30 9:00 9:30
P.M.

FIG. 8. Thermocouple recordings of heat loss in down-covered wood duck nest.

twice the drop in about half the time as compared to conditions on the warmer day. In 1950 when the female left the nest for nearly 10 hours, the outside temperature was much cooler (41°F.) than when this record was taken. This suggests a very drastic chilling of the eggs, probably to a point in the high forties. This occurred when the embryos were well advanced in development, the 14th day of incubation. Yet every one of the eggs hatched successfully although about 6 days later than the 1948 clutch.

These records may shed some light on the nature of conditions that can cause delayed hatching, in other words, prolonged incubation periods in the wood duck. Many other birds have been observed to have markedly varying incubation periods. Nice (1943) reports Campbell's observation that a "female Lyre bird incubated her single egg for 7 weeks before it hatched, but was off the nest from 7 to 8 hours each day." She adds that, "An egg placed under a fowl hatched in 4 weeks." It consequently appears that the extent to which incubation may be prolonged is a very variable quantity.

On the other hand no such indefinite speeding up of development is possible by increases in temperature. Romanoff (1934) found an increased rate of growth and percentage of hatch of pheasants and bobwhite embryos up to 102.5°F. but a rapid retardation above this, dropping to zero at 105°F.

A variable incubation period, then, may or may not extend for considerable periods beyond a minimum period but cannot under any circumstances be made shorter than this rather definite minimum. The minimum period would ideally be attained if a bird could incubate uninterruptedly or with numerous short periods of inattention (Kendeigh, 1940) for the entire period of embryonic development. Since this, of course, is rarely attained in nature, it would appear that the nearest to this relatively stable minimum incubation period obtainable as characterizing a species would be the shortest one to be authentically reported. Thus, in place of indicating the wood duck's incubation period from these records as being "from 25 to 31 days", it would seem better to state it as "25 days or longer." And it is my suggestion that other birds' incubation periods be stated in this way, thus placing the emphasis on the minimum length of the period as being the most significant datum.

SUMMARY

An automatic apparatus recorded nest activity from a floating floor in a wood duck house. Laying of eight eggs in 1949 occurred between 5:00 and 8:00 on successive mornings. Time female spent on the nest during egg-laying varied from 8 minutes to 3 hours and 11 minutes; average, one hour and 48 minutes. Nest attentiveness was recorded for 1948, 1949, and 1950. A definite tendency for the bird to sit closer on cool days was recorded. Normal time off the nest per 24 hours varied from 13 minutes to 4 hours and 40 minutes. The effectiveness of the down blanket was checked by thermocouple terminals cast into a plaster of Paris egg which was screwed in position in the nest. In one period when the female was off the nest for 1 hour and 22 minutes with outside temperatures of 63°F.-61°F. the nest temperature dropped 13.5°F. A study of chilling due to disturbances driving the incubating bird off the nest indicated that the shortest incubation period (25 days) was recorded during the season when no major disturbances occurred. Incubation periods of 29-30 and 31 days were recorded on years when serious chilling of the eggs occurred. It is suggested that the shortest incubation period for any species approaches most nearly the period characteristic of the species since any temperature rise above normal will not

shorten the period, but severe chilling can greatly increase the incubation period.

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INTERPRETATION OF BODY-SCALE REGRESSION FOR COMPUTING BODY LENGTH OF FISH [1]

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Methods of estimating body length of a fish from a given scale measurement are well known and have been reviewed many times (Lagler, 1952; Schuck, 1949; Van Oosten, 1929). All of these methods depend upon the correlation between body length and scale measurement. A correlation measures the degree of relationship of two variables having a common background or association. In the procedure of estimation, however, it is necessary to employ a regression. The use of a regression implies that one of the variables is independent and may be considered fixed. In the case of scale measurement and body length it is clear that two regressions may be derived, namely:

the regression of body length, L, on scale measurement, S, of the type,

$$L = a_1 + b_1 S \quad . \quad . \quad . \quad . \quad [1]$$

and the regression of scale measurement on body length of the type,

$$S = a_2 + b_2 L \quad . \quad . \quad . \quad . \quad [2]$$

Graphically the two equations produce lines which will coincide only if the correlation between body length and scale measurement is perfect (a correlation coefficient of 1). No such correlation has as yet been demonstrated for body-scale relationship. Since in growth computations the lengths at various ages are estimated from scale measurements, regressions of type [1] have been used by most investigators. Fry (1943) used a regression of type [2] which would be the proper regression to use for estimating scale measurements from body lengths but is less efficient than regression [1] for estimating lengths from scale measurements. For further discussion of the problems in choosing the proper regression see Winsor (1946).

Most growth calculations use the direct proportion or Dahl-Lea method where $L = bS$.

Buchanan-Wollaston (1936) pointed out that Lea's method of back-calculation is not a regression method. It is, on the other hand, based upon an assumption that the growth of the body and scale are directly proportional. It is usually recognized that this method gives an approximation since the body-scale regression rarely, if ever, passes through the O,O intercept. The use of this method assumes that the value of

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"a" in regression [1] is not great enough to significantly affect the computations. It would be of value in most cases to test this assumption. For general surveys and many management purposes growth approximations using the direct proportion computations are probably sufficiently accurate but it should always be recognized that they are approximations. Body-scale regressions differ for each species and probably for populations within species (Carlander, 1950a). Computation of regressions using small samples or even large samples with small size ranges might introduce more errors in the "corrected" growth computations than the errors resulting from the direct proportion assumption.

Where adequate samples are available, more accurate estimates of length can usually be made by plotting body length against scale measurements and then fitting the proper linear or curvilinear regression. It is doubtful that the body-scale regression is ever strictly linear but caution should be exercised in using a curve since a curve may be found to perfectly fit any particular sample, and the sample might not represent the population. The nature of the curve may be hypothesized from the sample. Further samples should then be taken to test the appropriateness of the curve for the population. If the sample is small or deviations from a straight line are slight, the additional work of computing a curvilinear regression might not be justified.

The body-scale regression is most often derived from mixed material. For example, the scales may be collected in different years, in different bodies of water, or from different year classes of fish. The formulation of a regression from such material involves the assumption that the regression is the same for all years, waters, or year classes in the study. The validity of the assumption needs further study. Mottley (1942) found no difference in the body-scale regressions of three year classes of rainbow trout, *Salmo gairdneri*. It has been shown, however, that the number of scales which a fish develops, and therefore the body-scale regression, may be modified by temperature, crowding, parasitism and perhaps other environmental factors during the early life of the fish (Hubbs 1927, 1941, Mottley 1934, Svärdson 1952). It may be expected that there will be differences in the body-scale relationships of fish in different year classes, or even to a greater extent in different bodies of water. In studies where a curvilinear body-scale regression has been described on the basis of one or two years' sampling, it is possible that much of the curvilinearity may be the result of differences in the body-scale regressions of the different year classes which are used in the various segments of the over-all regression.

In many age and growth studies regression [1] has been used to find an "adjusted" scale length by substituting the observed body length in the regression. The ratio between observed and adjusted scale measurement at the end of the scale is then used to adjust the scale measurement at each annulus. Finally, the body length at each annulus is estimated by substituting the adjusted scale measurement in the regression (Hile, 1941). There is an inherent inconsistency in this procedure (which will be referred to as procedure A). It should be emphasized that regression [1] estimates a body length from a given scale measurement and that regression [2] estimates the scale measurement for a given body length. Yet in this procedure regression [1] is used to estimate the scale measurement from length of the fish at capture and the observed scale measurements are then "corrected."

Another procedure (B) appears to be more correct mathematically. Estimated body lengths can be obtained for each observed scale measurement from [1]. The ratio between observed and estimated body lengths at the time of capture is then used to find adjusted body lengths at each annulus.

With procedure A it is said, in effect, that if the scale were 10 per cent larger when the fish was caught than the average scale for that size of fish, the scale would be 10 per cent larger than normal throughout the life. Therefore, the scale size should be proportionately decreased before computing the lengths at each annulus. Procedure A, however, includes the inconsistent step of predicting scale size from the body-scale regression.

With procedure B, it is assumed that if a fish at time of capture were 10 per cent smaller than the average fish with that size of scale, the fish would be 10 per cent smaller than the expected length for the size of that scale throughout life.

The computed body lengths are the same with either procedure if a straight line regression is used, but procedure B more clearly demonstrates what is accomplished by using the regression. If the regression is curvilinear, the computed body lengths usually will not be the same if computed by the two procedures.

When the regression is curvilinear it becomes apparent that procedure B does not take advantage of an assumption sometimes mentioned as necessary in the computation of growth from scales, namely, that the estimates of body growth are related to the proportionate growth of the scale and not to the absolute size of the scale. In other words the ratio between the distance to any annulus and the distance to the edge of the scale should be the same for each scale on the same fish. This assumption needs more critical examination.

It is questionable whether it is necessary to assume that the growth computations are entirely independent of the absolute size of the scale. In fact, Mottley (1942) suggested that back calculations from scale measurements could be entirely dispensed with in many situations and he demonstrated that differences in growth of various year classes of rainbow trout could be shown by comparing the actual sizes of the scales at various annuli.

The following experiment suggests that lengths at previous annuli can be more efficiently estimated from the proportionate growth of the scales than from the absolute size of the scales at various annuli. Ten scales were taken from each of 5 areas on a 170 millimeter (standard length), age group II, yellow bass (*Morone interrupta*) a species with fairly uniform scalation and with easily recognizable annuli. The 5 areas may be described as follows:

Area 1. Below the lateral line, even with end of pectoral fin.

Area 2. Above the lateral line, even with anterior edge of dorsal fin (slightly anterior of Area 1).

Area 3. Above the lateral line, even with anterior edge of soft dorsal.

Area 4. Below lateral line, even with anal fin.

Area 5. Nape, above the opercle. (Selected as an area with a greater range of scale size.)

The radii to the annuli and the edge of each scale were then measured at a magnification of 50 diameters (Table 1). The lengths of the fish at each annulus formation were then computed by two methods. In the first method, the regression method, it is assumed that body length can be estimated from the actual scale size at the annulus, as suggested by Mottley (1942). For the Clear Lake yellow bass population, from which this fish came, a straight-line body-scale regression with an intercept at 16 millimeters has been used for growth computations (Carlander, Lewis, Ruhr, and Cleary, 1953). Since the average scale radius for all 5 areas was 187.2 millimeters, the regression used in computing the lengths at the first and second annuli was:

$$L = 16 \text{ mm.} + 0.82R$$

where L = computed standard length

R = scale radius

and $0.82 = \frac{170-16}{187.2}$.

In the second method, the proportional method, it is assumed that the body growth is related to the proportional growth of the scale and not the absolute size of the scale. The lengths were computed from the following formula:

$$L = 16 \text{ mm.} + \frac{R_1}{R_c}(170-16)$$

where R_1 = radius at the annulus

and R_c = radius at capture.

It is obvious (Table 1) that the computed lengths by the proportion method are much more consistent from area to area than are those computed by the regression method. For the first annulus the range of the means is 7.2 millimeters for the proportion method and 27.1 for the regression method; for the second annulus, the ranges are 7.3 and 44.8 millimeters respectively. There is also evidence that the variation is less within each area for the proportion method than for the regression method. In 9 of the 10 cases, the coefficient of variation is less for the proportion method data than for the regression method.

If the body growth were strictly proportional to the scale growth, the computed lengths by the proportion method should be the same for scales from each area. Analysis of variance indicates a significant difference between the mean computed lengths at the first annulus (an F value of 4.74) and at the

TABLE 1.—DATA FOR COMPARISON OF LENGTHS OF FISH COMPUTED FROM ABSOLUTE SCALE SIZE AND FROM PROPORTIONATE GROWTH OF SCALES; SCALES WERE TAKEN FROM DIFFERENT LOCATIONS ON THE SIDE OF A YELLOW BASS

Location of scales (see text)	1	2	3	4	5
Scale radius					
Mean	218.7	177.3	193.6	197.5	148.7
Sum of squares	478,605	315,897	375,004	390,381	224,539
Coefficient of variation	.027	.085	.024	.030	.131
Computed length at first annulus by regression					
Mean	89.3	72.7	80.7	85.4	62.2
Sum of squares	80,019	52,989	65,243	73,026	39,130
Coefficient of variation	.062	.054	.045	.037	.113
by proportion					
Mean	78.8	76.5	78.6	81.4	74.2
Sum of squares	62,240	58,575	61,920	66,328	55,162
Coefficient of variation	.051	.031	.050	.033	.031
Computed length at second annulus by regression					
Mean	153.1	122.7	136.4	142.8	108.3
Sum of squares	234,621	151,419	186,124	204,008	118,843
Coefficient of variation	.033	.080	.021	.022	.121
by proportion					
Mean	134.3	129.1	133.2	136.4	129.4
Sum of squares	180,461	166,767	177,450	186,062	167,550
Coefficient of variation	.025	.026	.013	.008	.026

second annulus (an F value of 13.1). If area 5 is eliminated, the difference between the remaining means is not significant for the first annulus (an F value of 2.01).

Although the assumption that the body growth is strictly proportional to scale growth is not met, it is apparent that this assumption gives a better approximation than can be secured by relying upon absolute scale size and the regression method. Analysis of variance of the lengths computed by the regression method gave F values of 49.5 for both the first and second annuli. Taking all areas together, the variance at the first annulus is 20.1 for the proportion method or only 17.2 per cent as much as the variance for the regression method, and at the second annulus is 15.2 or only 4.9 per cent. Thus, it would take about 6 to 20 times as large a sample to estimate with equal accuracy the length of a fish at a previous annulus by the regression method as by the proportion method if the scales were taken from these areas indiscriminately. The variances of the samples computed by the proportion basis were 53, 38, 119, 72, and 24 per cent of the variances of the samples computed by the regression method for areas 1 to 5 respectively for the first annulus, and 43, 11, 38, 13, and 7 per cent for the second annulus. Even when the scales are taken from one area, larger samples are required to estimate the lengths by the regression than by the proportion method.

In populations where the body-scale regression has been adequately described and where scales are taken from the same area of the body, the use of absolute scale measurements are undoubtedly satisfactory and less laborious for comparing growth. Mottley has suggested that field measurement of the fish is unnecessary. The scale measurements have greater variances than the body measurements but equal accuracy may be attained by collecting a larger sample of scales. Tests should also be made to determine that the body-scale regression remains the same throughout the period of study.

With the regression method, the variances of a mean calculated length may be due to:

1. Differences in growth of the individual fish.
2. Deviations of the individual fish from the "normal" body-scale regression.
3. Deviations of the examined scale(s) from the average for the individual fish.
4. Errors in locating and measuring annuli.

The back-calculation methods attempt to reduce the variation due to the second and third reasons. The deviation of the scale measurement at time of capture from the "normal" scale size for a fish of the given length is measured and the scale measurements at each annulus (Procedure A) or the computed lengths at each annulus (Procedure B) are adjusted proportionally. However, with Procedure B and a curvilinear body-scale relationship, the adjustment may not be really proportional to the scale growth. A large scale and a small scale each with annuli at 0.4, 0.6, and 0.8 of their scale radii would give different growth histories because the slopes of the curve where the adjustments would be made would probably be different. In fact, the same scale if projected at a different magnification would give a different growth history. Of course this latter situation can be easily avoided by using only one magnification or by correcting the scale measurements to the same magnification as that used in computing the body-scale curve.

Neither Procedure A nor B appears to be entirely satisfactory in estimating body growth from scale measurements when the body-scale relationship is not assumed to be linear. Procedure A includes a step of estimating scale length from the regression of body length on scale measurements (regression 1) and Procedure B does not take advantage of the assumption that body growth is more closely correlated with proportional growth of the scale than actual scale size. Probably the resulting errors with either method are fairly small in proportion to the computed lengths. Since the refinements of a curvilinear regression can be used only with fairly large samples representing all size classes, the straight regression method of computing length at various annuli may be the most satisfactory when a curvilinear regression is used.

Although further analytical investigation of the body-scale relationship and the assumptions upon which growth computations are based is needed before the questions raised in the present paper can be fully answered, there is a practical reason for discussing the problem at this time. In some studies (*e.g.* Carlander, 1945a, 1945b, 1950a, 1950b; Cleary, 1949; English, 1952; Erickson, 1952; LeCren, 1947; Lewis, 1950; Lewis and Carlander, 1948; Parsons, 1950; Segerstrale, 1933; Sigler, 1949; Tate, 1949; and Van Oosten, 1942), as a shortcut or in an attempt to give more weight to small samples at both ends of the distribution, the fish have been grouped by lengths and the regression fitted to the average scale measurement for each group. The effect is to plot the points along the line [2], which is the wrong regression, and then to fit the regression with formula [1]. The estimate of the intercept arrived at will coincide with a_1 only if the correlation coefficient is 1. If it is desired to group the fish, it would be preferable to separate them according to scale measurements and to find the average body length for each scale measurement group. The difference in procedure may be demonstrated in any body of data in which the correlation is not perfect. Even though the relationship of the body-scale regression to growth computations still needs elucidation, it is obvious that it is erroneous (although the errors may be small) to fit the regression of body length on scale measurements by using mean scale measurements at fixed body lengths.

The computation of a body-scale regression assumes that variance of body lengths is the same for each scale length (Anderson and Bancroft 1952, p. 160). More likely the variances of the body lengths increase as the scale size increase, as demonstrated in Table 2. Mottley (1942) showed that the variances of scale lengths are correlated with body lengths. Snedecor (1946, pp. 448-451) suggests the transformation of the data to logarithms when the variance of the dependent variable is correlated with the independent variable as in this case. Such a transformation eliminated the correlation in the data of Table 1. The use of the logarithmic transformations would greatly increase the labors of computing lengths since the scale measurements must all be converted to the logarith-

TABLE 2.—VARIANCES OF STANDARD LENGTHS OF BLUEGILLS (*Lepomis macrochirus*) AT VARIOUS SCALE SIZES, IN NUMERICAL SCALE AND ON LOGARITHMIC SCALE. EACH SAMPLE INCLUDES 6 FISH COLLECTED AT EAST LAKE, CHARITON, IOWA, 1948

Scale radius	Variance of body lengths	Variances of log body lengths	Log of scale radius	Variance of log body lengths
7–9	.38	.034	.88–.98	0.019
10–12	.31	.012	.99–1.09	0.018
13–15	.36	.007	1.10–1.20	0.005
16–18	.66	.012	1.21–1.31	0.016
22–24	.76	.012	1.32–1.42	0.014
55–57	.67	.003	1.66–1.76	0.004
104–106....	3.33	.008	1.77–1.87	0.032
110–112....	.73	.002	1.88–1.98	0.004
173–175....	5.70	.005	1.99–2.09	0.024
176–178....	1.96	.002	2.10–2.20	0.028
180–182....	7.67	.007	2.21–2.31	0.004
186–188....	10.58	.010	.....	.....
191–193....	5.85	.004	.....	.....
Coefficient of correlation, r_1	.813	—.521		.057

mic scale. Fry (1943) describes a nomograph which simplifies these conversions. Probably in most growth studies it is sufficiently accurate to dispense with the logarithmic transformations and to disregard the assumption that the variances of the body lengths are the same for each scale length.

SUMMARY

1. The regression of body length on scale measurement appears to be the proper regression to use in describing the relationship between body and scale for growth computations.

2. The usual use of the regression to find "adjusted" or "normal" scale measurements from which the lengths at various annuli can be computed involves the estimation of scale measurements from lengths with the body-scale regression when the scale-body regression would be more efficient and accurate for such estimation.

3. An alternative procedure, estimating the body lengths from scale measurements and then "correcting" for deviations of scale size from normal, appears to be more logical.

4. Either procedure gives identical results if the body-scale regression is linear.

5. The use of a curvilinear body-scale regression introduces difficulties in interpretation since it does not take advantage of the assumption that body growth is related to proportionate growth of the scale rather than to absolute size of the scale.

6. Scales from a yellow bass indicated that the variances of body lengths estimated from proportionate growth of scales were much less than those for lengths estimated from absolute scale size.

7. The use of the regression method without the correction or "normalization" of scale size may be quite satisfactory where the body-scale relationship has been adequately described and where samples are fairly large. With a curvilinear regression, it may be the only sound procedure.

8. The practice of averaging scale measurements at various body lengths to compute the body-scale relationship is erroneous. If the data are to be grouped, the mean body lengths at various scale measurements should be used.

9. Computation of the body-scale regression, without logarithmic transformation, probably usually involves disregarding the assumption that the variances of the body lengths are the same for each scale length.

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NESTING AND PRODUCTION OF THE BLUE-WINGED TEAL (*Anas discors* Linnaeus) IN NORTHWEST IOWA [1]

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This study of the blue-winged teal involved observations made in northwest Iowa during August and September in 1947, from March 14 to September 1 in 1948, and, except for 12 days during the middle of August, from March 18 to September 1 in 1949.

In making the study, four objectives were kept in mind: (1) to develop a method of estimating yearly production prior to the shooting season; (2) to compare present with past production on the same areas as a basis for determining waterfowl population trends; (3) to identify and analyze factors affecting the blue-winged teal in Iowa; and (4) to develop waterfowl management recommendations for northwest Iowa.

Particular appreciation is due Dr. H. M. Harris, Head, Department of Zoology and Entomology for guidance and counsel. The leadership of Dr. Thomas G. Scott during the early phases of the study, and of Dr. Edward L. Kozicky and Dr. George O. Hendrickson, who directed the project to completion is acknowledged. The advice and aid of Dr. Logan J. Bennett was helpful. Special thanks are due Drs. Paul L. Errington, H. H. Knight, E. A. Hicks, and J. M. Aikman, all of Iowa State College, for their constructive criticisms.

The hearty cooperation of District Game Manager B. I. Severson, Conservation Officer Ben Jackson and Game Biologist James Sieh aided the study. Mr. Tom Eilers of Storm Lake and the members of the Fort Dodge Gun Club kindly permitted observations to be made on their property. Appreciation is expressed to Mr. L. C. Michael, Bill Michael, Lee Fredericks, and Dean Christianson for their interest and help during the project, and to the 4-H boys of Lake Center High School for their assistance in extinguishing grass fires on Dewey's Pasture in 1949. Mr. Richard Moran was employed as a field assistant during the summer of 1949.

The Research Area

The "Ruthven Area" (Figure 1) was selected for this investigation because comparisons could be made with past studies in that area. The data presented in this study were recorded from observations around Dan Green's Slough, Trumbull Lake, Round Lake, Dewey's Pasture, Smith's Slough, Mud Lake Slough, Mud Lake, Lost Island Lake, Johnson's Slough, Brown's Slough, Barringer's Slough, and Whitford's Slough in Clay and Palo Alto Counties and Twelve-Mile Slough in Emmet County. The 1947 and 1948 seasons were devoted to an intensive study of nesting in Dewey's Pasture and Smith's Slough. Throughout the 1949 season an effort was made to study as many nesting areas as possible in order to obtain quantitative data.

The topography of Clay and Palo Alto Counties is characteristic of the Wisconsin glacial drift sheet. In general, the marshes, sloughs, and meandering streams tend to lie in a north-south direction. Drainage flows southwesterly into the Little Sioux River in Clay County or towards the east into the Des Moines River in Palo Alto County. According to Stevenson and Brown (1919 and 1922), five swamp and bottomland soils cover 17.2 per cent of Clay County and 26.1 per cent of Palo Alto County. Since 1919 there have been numerous drainage operations in Clay and Palo Alto Counties with the result that only about 4 per cent of the area is now marsh land.

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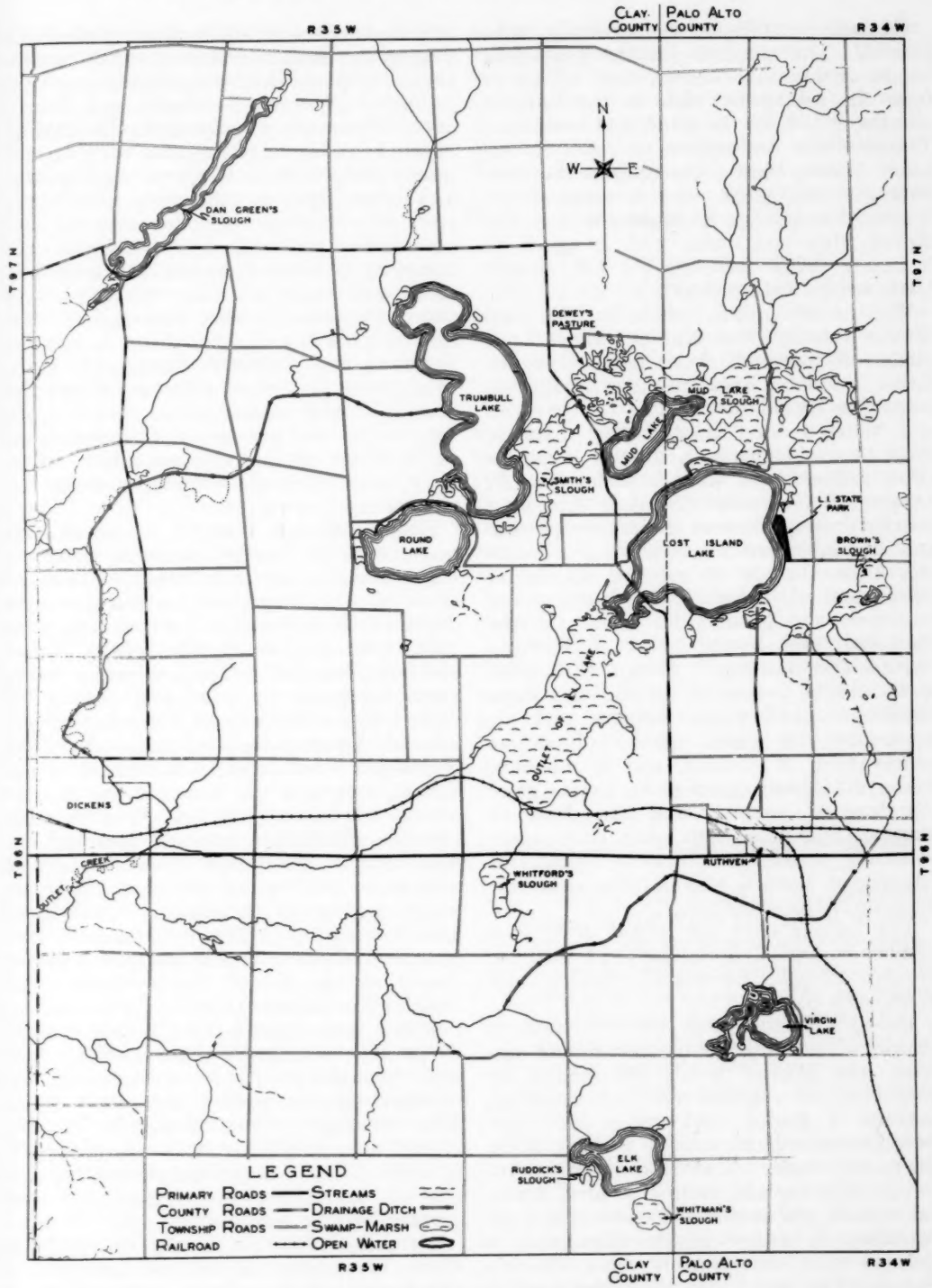
[2] Now with Branch of Game Management, Fish and Wildlife Service, U. S. Department of Interior, Washington 25, D. C.



THE RUTHVEN AREA, IOWA.

FIGURE 1

Climatic conditions are typically continental. The direction of the prevailing winds during fall, winter, and spring is from the northwest, while in the summer months, it is from the south and southeast. Temperatures are subject to rapid fluctuation. During these investigations the temperatures fluctuated over a range of 80 degrees Fahrenheit. Most of the rain fell during May and June, with as much as 5 inches being recorded for one month (Lamoureux, 1948 and 1949).

The native prairie, which at the turn of the century was still prominent, has almost disappeared. Small patches can be found in isolated areas unsuited for agriculture. The dominant plant in the pastures and untilled land around the marshes, lakes, and sloughs is Kentucky bluegrass (*Poa pratensis*) or Canada bluegrass (*P. compressa*). Goldenrod (*Solidago* spp.) and hoary vervain (*Verbena stricta*) are present and are indicators of overgrazing or burning. Dense stands of ragweed (*Ambrosia trifida* and *A. artemisiifolia*) occur along fencerows and in irregular areas. On the protected, state-owned areas of Dewey's Pasture and Barringer's Slough, such relics of the native prairie as the tall and short bluestems (*Andropogon furcatus* and *A. scoparius*), the grama grasses (*Bouteloua curtipendula, B. gracilis,* and *B. hirsuta*), wild rye (*Elymus canadensis*), Indian grass (*Sorghastrum nutans*), and the dropseed grasses (*Sporobolus* spp.) are once again becoming established. Western wheatgrass (*Agropyron smithii*) also is quite abundant on some of the study areas.

The nesting data are largely from four distinct ecological units: Dewey's Pasture, Smith's Slough, Barringer's Slough, and Whitford's Slough.

Dewey's Pasture is a 400-acre tract of prairie with bluegrass on the rolling upland, and shallow ponds surrounded by sedge-meadow vegetation in the numerous hollows. A graded road and a low ridge form the main physiographic features along the north border. Mud Lake, a privately-owned shooting and recreation area, forms the eastern and southern borders. The west boundary is a low gentle ridge, and a county road separates it from Smith's Slough. The water depth of the various ponds varies up to 3 feet. Hard-stemmed bulrush (*Scirpus acutus*) and cattail (*Typha latifolia*) dominate the deep-water emergent vegetation. Shallow-water emergent vegetation is composed chiefly of sedges (*Carex* sp.), cordgrass (*Spartina pectinata*), and sloughgrass (*Beckmannia syzigachne*). The upland vegetation is mainly bluegrass, with various prairie forbs, such as hoary vervain, greater and lesser ragweed, goldenrod, aster (*Aster* sp.), sweet clover (*Melilotus alba* and *M. officinalis*), and milkweed (*Asclepias* sp.) occurring in isolated patches. Three earthen dams tend to stabilize the water levels in two of the pond systems. Drainage or overflow is southeast to Mud Lake or west to the north end of Smith's Slough. No cattle were grazed on Dewey's Pasture during the period of this investigation. Three grass fires, one in 1948 and two in 1949, destroyed much of the upland vegetation that might have been utilized by puddle ducks as nesting cover.

Smith's Slough consists of about 500 acres and is located between Dewey's Pasture on the east and Trumbull Lake on the west. The slough with an average water depth of about 14 inches is a long triangular basin with borders of low rolling prairie and cultivated fields. The deep-water emergent vegetation is composed mainly of cattail and soft-stemmed bulrush (*Scirpus validus*). Floating mats of spikerush (*Eleocharis* sp.) cover much of the center of the slough. Emergent vegetation in the shallow water consists mostly of river bulrush (*Scirpus fluviatilis*) bur-reed (*Sparganium* spp.), sedges, and slough grass. The upland vegetation is about 60 per cent bluegrass, sedges, and weeds (*Solidago* spp., *Aster* spp., and *Cirsium* sp.) The remaining 40 per cent is in alfalfa and occupies the northeast corner of the slough. Water drains into Smith's Slough from Dewey's Pasture and as overflow from Mud Lake. The water level in Smith's Slough is maintained by two metal-pile dams on the west side and the overflow enters nearby Trumbull Lake. Four to eight cattle ranged in Smith's Slough during 1948 but none was permitted in 1949. This is a privately-owned slough that is maintained for recreational and private hunting purposes.

Barringer's Slough, locally called "The Outlet", comprises about 1,000 acres and is the largest of the state-owned waterfowl nesting areas. The northern portion of Barringer's Slough is bounded by Lost

Island Lake and cultivated fields. Low moranic terrain and level marsh characterize the general topography along the eastern side of the slough. An east-west ridge, which rises rapidly from an extensive marsh plain, forms the southern boundary. A broad northeast-southwest ridge rises gradually on the west side of the slough and forms the major physiographic feature there. An island approximately 30 acres in size separates the slough into two unequal portions with the southern part comprising about 70 per cent of the total area. About 320 acres of the slough is open water varying in depth from 1 to 4 feet. Extensive growths of cattail are present on the broad shallow flats and also in the deeper water around the openings. An irregular band of sedge-meadow vegetation forms the connecting link between the cattails and the upland cover. The predominant upland vegetation is bluegrass but, where it does not form a solid cover, a mixture of herbaceous vegetation such as greater and lesser ragweed, bur marigold (*Bidens* sp.), goldenrod, aster, and mint (*Mentha* sp.) is present. The major inlet of water to Barringer's Slough comes from the outlet dam at the south end of Lost Island Lake. Other minor sources are a small creek draining the land on the east side of the slough and the overflow from Whitford's Slough, which drains north to enter the south bay. Several drain tiles empty into Barringer's Slough but surface runoff and deep seepage apparently contribute most of the stored water. A low-head concrete dam at the southwest end of the slough tends to stabilize the water levels. Approximately 40 per cent of the area which provided acceptable cover to the nesting waterfowl was grazed.

Whitford's Slough comprises about 125 acres of marsh and rolling upland located south of Barringer's Slough and 3.5 miles west of Ruthven on U. S. Highway 18. About 10 per cent of the area is open water with an average depth of approximately 12 inches. Hard-stemmed bulrush dominates as a deep-water emergent. Sedges, slough grass, cordgrass, bur-reed, and river bulrush composed the bulk of the shallow-water emergents. The upland vegetation is predominantly bluegrass but overgrazing has caused numerous patches of lesser ragweed, thistle, goldenrod, and hoary vervain. In 1949 a low earthen dam was constructed at the north end in an effort to maintain water for the cattle and muskrats. All of Whitford's Slough is grazed, but because of the location of salt blocks near the highway, some areas at the south end of the marsh were relatively untouched. Whitford's Slough is a privately owned marsh that provides pasturage for dairy cattle in the summer and muskrat trapping in the winter.

TECHNIQUES AND METHODS

During spring migration, the lakes and marshes of Clay and Palo Alto Counties near Ruthven were checked daily for waterfowl, and sex ratios of the different migratory species were recorded.

To obtain nesting data, it was necessary to search systematically, on foot or by boat, all of the emergent and upland vegetation surrounding the marshes and sloughs. Two Chesapeake Bay retrievers, trained to work the cover or on a dragline, assisted in locating duck nests. Another aid was the association of males on their "waiting stations" with females and their nests.

The yearly production of waterfowl was obtained from data on nest densities, nest success, and brood counts. The following procedure, as outlined by Bennett (1938), was used in determining the year's production:

1. Determine the total number of nests in the area.
2. Determine the percentage of successful nests.
3. Multiply the number of successful nests by the mean number of hatched eggs in the successful nests to determine the number of ducklings.
4. Multiply the mean number of young observed with the adult females [which was assumed to indicate the number of young reaching the migratory age] by the total number of successful nests.

The relative success of the investigator in locating duck nests was dependent upon several factors: (1) time of day; (2) stage to which incubation had advanced; 3) density and height of nesting cover and surrounding vegetation; (4) velocity of the wind; and (5) air temperature at the time of search.

Available duck nesting cover was searched during all hours of the day, with greatest

degree of success achieved during mid-morning.

The degree to which incubation had advanced seemed to be the most prominent factor that affected the success of locating nests. Usually blue-winged teal females flushed from the nest or very near it, and the nest could be found by carefully searching the cover in the immediate vicinity from which a female flushed.

During early incubation or egg-laying, females flushed from their nests at greater distances from the observer than after incubation had been in progress for some time. The available nesting cover was traversed back and forth at intervals of about 5 to 10 yards during the period when most of the females were laying eggs. With the onset of incubation, it was necessary to reduce this interval to about 4 to 6 yards. As the time of hatching approached, the interval was further reduced to 2 or 3 yards.

Toward the end of the nesting season, the density and height of the cover utilized for nesting increased. For the most part, the early nests were located in cover which had formed prominent clumps and tufts, whereas the late season nests were situated in cover with a homogeneous appearance. Incubating females did not flush readily from nests within a few days of hatching.

A wind velocity of from 5 to 10 miles per hour seemed to aid in the search for nests. By advancing into the wind, any splashing of water or noise that the observer made was carried away from the female on the nest. It also aided the dogs' ability to scent nests. Winds of higher velocity than 15 miles per hour tended to reduce the success of finding nests, for vegetation was blown over nests, and scent from nests was quickly dispersed and blown away.

On cool days (maximum temperature less than 75 degrees Fahrenheit) the efficiency of the investigator and the bird dogs increased. Generally the dogs were unable to scent incubating females or unattended nests on hot afternoons (maximum temperature more than 85 degrees Fahrenheit).

A check on the success of the investigator in finding waterfowl nests on land was made possible when in 1948 about 75 per cent, and again in 1949 about 50 per cent, of Dewey's Pasture was "stripped" for bluegrass seed. During both years, only two additional nests were found at the time of stripping that had not been located previously, which indicated that from 65 to 70 per cent of the duck nests were found.

Analysis of the nesting cover utilized by the blue-winged teal was made by 1/4,000-acre quadrats (Figure 2). Strips of hardwood ½ by 1 inch and slightly over a meter in length were used in marking out quadrats. Each quadrat was oriented with the duck nest as the center and the four sides of the quadrat extending toward the cardinal headings of the compass. Plants present within the quadrat were listed with reference to their area, density, height, and species composition. Two plots 1 foot square were selected at random in the corners of the quadrats, and the plant species in these plots were listed by frequency and basal area. A Weston Master II universal exposure meter was used to measure and compare the light intensity in the nest with that of the open sky directly above the nest.

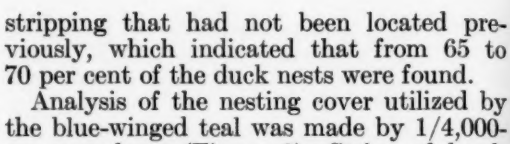


FIG. 2. Quadrats, 1/4,000 acre in size, were used to obtain data for the analysis of blue-winged teal nesting cover. Each quadrat was oriented with the duck nest as the center.

PRENESTING ACTIVITIES

About 60 per cent of the first groups of spring migrant blue-winged teal to arrive in the Ruthven Area during 1948 and 1949 were paired. However, the males tended to outnumber the females approximately 2:1 and courting was common. As the mating season approached (April and May), courtship became more ardent with groups of 4 to 8 males pursuing one female. In these large courting groups, the female exhibited no apparent partiality for any particular

male. The males attempted to crowd about her and spent much of their time chasing each other away from her. In some instances, the female tried to evade the amorous males by dodging, swimming rapidly through the water, or flying for a short distance. In other cases, females were observed to chase an overamorous male but the male quickly returned and was accepted with as much favor as other suitors.

Much of the courtship process took place in nuptial flights, which coursed over and around the water areas. Nuptial flights of blue-winged teal were noticed soon after the birds arrived in the Ruthven Area. During the latter part of March, the sex ratio in these flights varied from 4 to 5 males to 1 female. As the migration progressed during the first few weeks of April, this ratio was reduced to 2 or 3 males to 1 female. By mid-April and on into May, most of the birds were paired but an occasional flight of three (2 males and 1 female) was observed. Tabulation of the sex leading the flights throughout the months of March, April, and May revealed that the early flights in March were predominantly led by males but as soon as the nesting season approached and more paired flights were observed, the females led (Table 1). Mate

TABLE 1.—CHRONOLOGICAL SEX RATIO CHANGE IN BLUE-WINGED TEAL FLIGHTS DURING MARCH, APRIL, AND MAY

Month	No. Male-led	No. Female-led
March	19	7
April	15	36
May	8	28

selection appeared to be a process whereby single males were gradually eliminated from the courting group until only one male remained with the female. Two observations made of mate selection indicated that the process might progress rapidly at times and be accomplished in a few hours.

Any unescorted female blue-winged teal was quickly approached by courting males and a courting group resulted. Females which apparently were sexually receptive returned the "head-pumps" of suitors. Courting antics took place on shoreline, beaches, and mud flats as well as in the air. The mating routine and copulation occurred on the water.

Mated males actively defended "waiting stations", which appeared to be a variation of territory as defined by Pettingill (1947). For the purpose of this investigation, a "waiting station" was defined as a site occupied by the male while the female was building the nest and depositing the eggs. It was often maintained into the early stages of incubation.

Of 111 observations of courting blue-winged teal, 90 per cent were recorded as occurring in the shallow-water emergent cover types, 7 per cent on open water, and 3 per cent along shoreline. Small openings or sandbars in shallow-water emergent cover were utilized extensively as courting places.

NESTING

After a series of censuses on Dewey's Pasture, Smith's Slough, Barringer's Slough, and Whitford's Slough, the estimated 1948 breeding population of waterfowl on these areas was as follows: blue-winged teal, 120 pairs; common mallard (*Anas p. platyrhynchos*), 20 pairs; redhead (*Aythya americana*), 25 pairs; ruddy duck (*Erismatura jamaicensis rubida*), 40 pairs; and American coot (*Fulica americana*), 200 pairs. Except for the coots and redhead, there was an increase in 1949 in the breeding population of all of the above species. Approximately 140 pairs of blue-winged teal, 50 pairs of mallards, 25 pairs of redheads, 50 pairs of ruddy ducks, and 125 pairs of coots remained to nest.

The numbers of blue-winged teal using the Mississippi Flyway steadily decreased from 1946 to 1948, but a slight increase was shown in 1949 (U. S. Fish and Wildlife Service, 1949). Bennett (1938) indicated that the nesting population in the Ruthven Area varied from 60 to 110 pairs from 1932 through 1936. Hansen (1947) estimated the 1946 breeding population of Barringer's Slough as 128 pairs. The teal nesting population evidently has varied from year to year and probably has reflected the amount of habitable environment in the area. Thus the Ruthven Area has tended to carry its capacity of nesting waterfowl each year with slight regard to the fluctuations of the Flyway populations.

The distribution of nesting teal was not

uniform during any particular year. The nesting density on Dewey's Pasture in 1948 was one nest per 30 acres, whereas in 1949 it was one nest per 14 acres. Over the 2,171 acres of potential teal nesting cover examined in 1949, there was one nest per 12.5 acres. The nesting density for 1,611 acres of bluegrass was one nest per 12.2 acres, and in sedge-meadow, one nest per 11.5 acres. The heaviest concentration of teal nests, one per 1.3 acres, was found on the 30-acre ungrazed island of Barringer's Slough in 1949. Bennett (1938) believed that the average nesting density on habitable marshes was one nest per 10 to 20 acres of margin.

Inspection of habitat by blue-winged teal for suitable nesting sites apparently took place as soon as the birds were paired. Much of the time during early morning and late evening hours was spent examining water areas. It appeared that the female selected the area within which the nest would be located, for the male tended to follow the female during her inspection tours. Sometimes the female would leave the male at the edge of the water area or on his "waiting station" for brief periods and walk around the margins and up into the grass, examining the habitat very closely. How long the inspection period lasted for any specific pair was difficult to determine, but it was believed that about a week was usual.

Early attempts at nest building were little more than scooped-out depressions in the soil. On two occasions, females were observed scratching out these depressions with their feet. These early attempts were generally about the size of a man's cupped hand. Not one instance was recorded in which a female blue-winged teal returned to nest in a particular site if she were frightened or disturbed in her nest building. Field observations on 63 females indicated that nest building occurred from 7:00 to 10:00 a.m.

The time taken to construct a nest varied from a couple of days to more than a week. In some cases, an egg was deposited in a freshly scratched depression. In other instances, the female spent several days making the depression and one or two more placing small bits of dried vegetation in the bottom before an egg was deposited. Of 173 nests, 39 were constructed and lined with old bluegrass, and 105 were similarly constructed but had quantities of down present. The remaining 29 nests were constructed of other plant materials and down. It was quite apparent that availability and the cover type in which the nest was situated determined the materials used. No evidence was found that the female had carried nest material from a far-removed location for nest construction. Dried vegetation was used to line the bottom and sides. Upon completing the grass lining, the female mixed down with loose bits of vegetation for the sides and a portion of the top. The bulk of the down was placed around the rim. The downy covering was pulled over the eggs when the female left the nest. The down, which the female plucked from her breast, was similar to miniature cotton balls that progressively changed from gray in the center to a brownish-blue at the periphery. Down was deposited in some nests as early as the laying of two eggs but, in 82 per cent of the 134 nests recorded with down, it was not incorporated in the nest materials until there were four or more eggs present.

Detailed measurements were taken on 173 blue-winged teal nests and partial data on 13 additional nests. (Table 2).

TABLE 2.—DATA OBTAINED FROM MEASUREMENTS TAKEN ON 186 BLUE-WINGED TEAL NESTS IN NORTHWEST IOWA DURING 1948 AND 1949

Measurements	Range (inches)	Number of Observations	Mean (inches)	Standard Deviation (inches)
Outside Diameter.....	5.0–11.0	186	7.7	0.56
Inside Diameter.....	3.5–8.0	186	5.3	0.78
Bowl Depth.....	1.0–4.5	186	2.2	0.58
Thickness Under Bowl...	0.5–3.0	186	0.8	0.38

Sixteen of 173 nests showed evidence of a ramp, and 119 of the 173 had canopies. Only 17 had eggs completely covered with down at the time of discovery. A total of 46 nests was located within a mean distance of 5.9 feet of a trail of some kind.

All blue-winged teal nests under observation were located at an elevation of more than 1 foot above the water level. The mean

elevation of 173 nests located was 2.9 feet with a range of 1 to 25 feet. Data recorded on the location of the nests indicated that 73 per cent of the nests were located about midway between the water line and the highest point of surrounding land.

Teal nests were found from 20 to 210 yards from open water. The mean distance for 186 nests was 79.4 yards. During May it was 71.6 yards, and in June it dropped to 63.3 yards. For the month of July, which was toward the end of the nesting season, it was 103.2 yards. Eighty per cent of the nests observed were located less than 100 yards from open water. Nests which were attended by the female when found, had a mean distance from open water of 75.4 yards while those nests which were destroyed or deserted were at a mean distance of 85.6 yards. In nesting cover dominated by bluegrass, the mean distance was 76 yards. In sedge-meadow nesting cover, it was 62 yards.

The nearness of one nest to another depended upon several factors, namely: the amount of suitable nesting cover available, the size of the breeding population, and whether the nest was a first nest or a renesting attempt. Two active nests involving two different females were found about 10 yards apart. For the most part, active nests were separated by distances greater than 50 yards. In the case of renests, it was judged from field observations that the same female built the second, third, and fourth nests within about 50 yards of the first. This was quite obvious when one checked map locations (Figures 3, 4, 5, and 6) of nests as well as time of

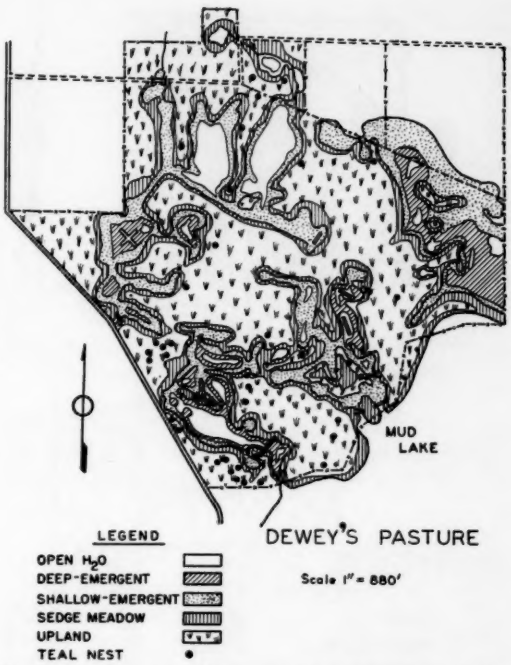


FIG. 4. Nest locations of blue-winged teal in Dewey's Pasture.

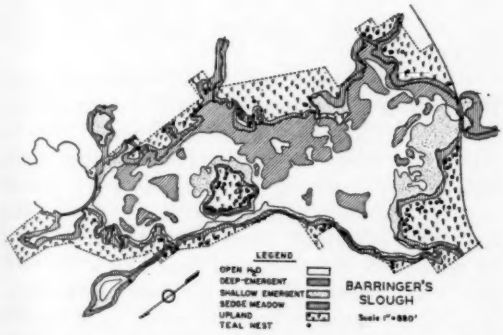


FIG. 3. Nest locations of blue-winged teal around Barringer's Slough.

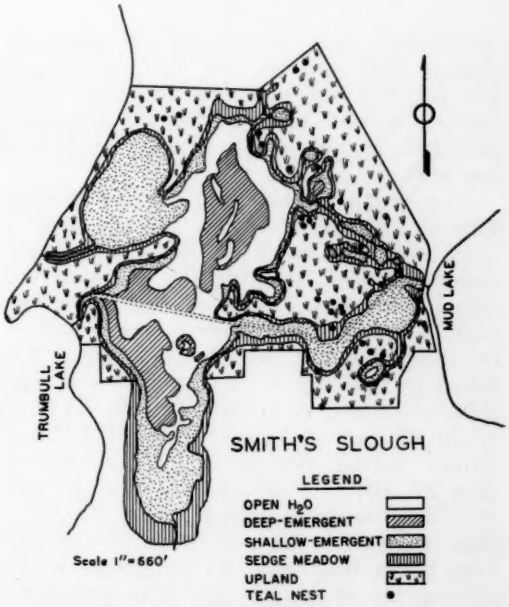


FIG. 5. Locations of blue-winged teal nests found at Smith's Slough.

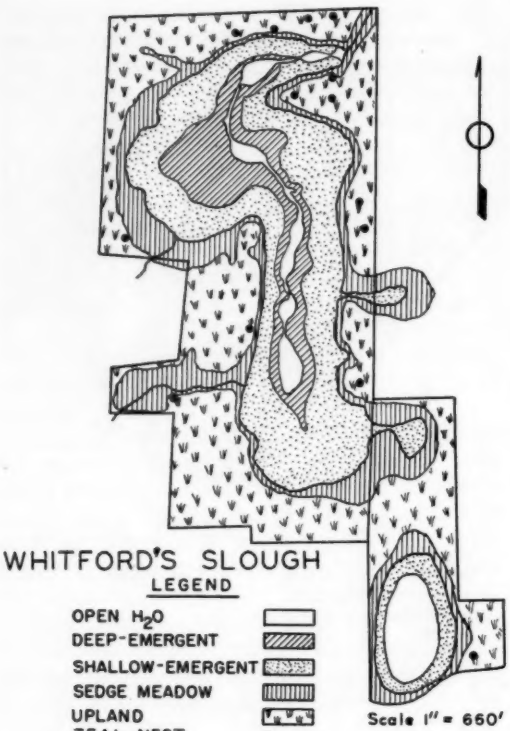


FIG. 6. Locations of blue-winged teal nests around Whitford's Slough.

destruction and beginning of renesting. During May and the first half of June, it was possible also to check the male on his waiting station and the female associated with him as well as the general location of her nest.

The length of the nesting season for the blue-winged teal was from the first week of May to the first week of August, a period of about 100 days. In 1948, the first nest was found on April 27 with one egg. Four eggs were laid in this nest before it was destroyed. On the morning of May 3, 1949, a nest was found in Barringer's Slough with two eggs, thus indicating that the first egg was laid about the first of May. The latest teal nest found during the investigation was on July 21, 1949. It contained nine eggs. This nest was later destroyed, but remaining eggs indicated that incubation had not been under way long. At the height of the nesting period, single eggs were frequently noticed but in most cases a thorough search of the cover in the immediate vicinity revealed either an active or destroyed nest. Whether these single eggs were laid away from the nest or whether a predator had scattered them about was not determined. Many of the single eggs were quickly destroyed and their presence might have been a factor in attracting predators to nests. It appeared, however, that once egg laying had begun few eggs were laid outside the nest.

Blue-winged teal eggs were creamy tan with little or no variation in shade. The shell was smooth and, as noted by Bennett (1938), slightly glossy during incubation. Bent (1923) gave the average measurements of 93 eggs in various collections as 33.4 by 46.4 millimeters. Measurements during this investigation of 142 blue-winged teal eggs gave a mean width of 33.9 millimeters ± 0.37 with a range from 30 to 37, and a length of 47.1 millimeters ± 0.75 with a range of 38 to 51. As near as could be judged from field observations, egg laying took place between 7:00 and 10:00 a.m. In the afternoon, nests were covered and females were commonly observed feeding and resting in the company of their mates.

A receptacle constructed by the female in which at least two eggs were laid was considered a nest. The number of eggs found in 186 teal nests varied from 2 to 13. The number of eggs being incubated varied from 7 to 13. Bennett (1938) stated that in 341 normal nests the average number of eggs per nest was 9.3 and in 27 renests the average was 4.3. The mean clutch size of 48 renesting attempts in 1949 was 6.4 eggs per nest. Of 699 eggs counted in 87 active nests, the mean number per nest was 8.0 while in 99 destroyed nests the mean was 5.4. The peak of egg laying occurred during the last week of May. A prominent renesting period occurred during the first half of July.

Female blue-winged teal were flushed from 63 of 186 nests. Figure 7 compares the frequency distribution of 63 flushed females with the time of day. Most of the nests located by flushing the female were found during the last two weeks of May and the first two weeks of June (Figure 8). A total of 64 active blue-winged teal nests, or 73.6 per cent, were located between 8:00 a.m. and 12:00 noon; whereas in the case of the destroyed nests, only 57.6 per cent were located during the same period of time.

FIG. 7. Number of females flushed from nests in relation to time of day.

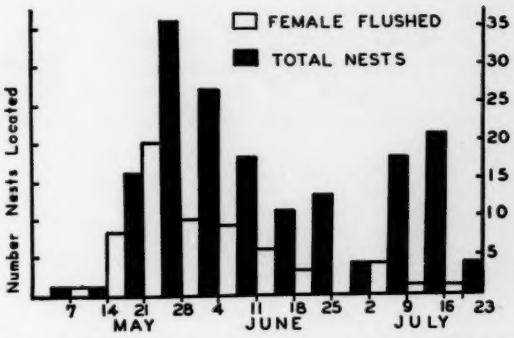


FIG. 8. Comparison of nests located by flushing females to total number of nests found.

After field observations indicated that searching for nests later than 2:00 p.m. brought diminishing returns for the hours expended, the searching time was narrowed to that period between 7:00 a.m. and 2:00 p.m. The greatest number of nests were located in the shortest period of time from 8:00 a.m. to 2:00 p.m. during the last two weeks of May and the first two weeks of June.

As near as could be determined, incubation began within 24 hours after the last egg was deposited. The female remained on the nest most of the time but usually left to feed or to rest from 6:00 to 7:30 a.m., from 2:00 to 4:30 p.m., and from 6:30 to 7:30 p.m. Females were observed to remain away from their nests from 30 minutes to 2 hours. On warm afternoons, the nests were often left unattended, but covered, for more than an hour and a half. The early morning and late evening resting and feeding periods were shorter than those near mid-day. Upon leaving the nest, whether of her own accord or when frightened, the female usually flew directly toward the male on his waiting station. As the hatching date approached, the female, if frightened, would fly but a short distance from the nest and land in the cover feigning injury, or would circle the nest uttering low quacks. In more than 75 per cent of the cases, the female defecated upon the eggs if she was disturbed while on the nest. The period of incubation varied from 21 to 23 days with the hatching of the last egg considered as terminating incubation.

In three instances, blue-winged teal nests were observed in the morning with several eggs pipping and by the end of the same day the young had hatched and left the nest. All egg caps from successful nests were similar in size and shape. Egg fragments left by predators did not have the cap shape. More than 75 per cent of the ducklings hatched between June 15 and 30 each year.

MALE WAITING TERRITORY

No data were obtained from observations on 186 pairs of nesting blue-winged teal that would indicate the male or female established or defended territories about their nests. However, males were observed to defend waiting stations during May and June when occasional trespass by other male blue-winged teal occurred. Not all of the waiting stations were found but in the main they were sufficiently prominent to associate 66 with 118 blue-winged teal nests found by the end of the first week of June. Approximately 23 per cent, or 15 nests, of these 118 later hatched successfully. Thirty-five of the 59 waiting stations were located near a prominent object, such as an old muskrat house, a sandbar, a rock, or a log. The proportion of shoreline covered by vegetation in the immediate vicinity of waiting stations varied from 26 to 100 per cent. Of 59 waiting stations, 54 were situated where more than 75 per cent of the shoreline was covered with vegetation. Only 3 per cent of the waiting stations were located in sparse vegetation; whereas, 42 and 55 per cent were recorded in medium and dense cover, respectively. The three major cover types and the number of waiting stations recorded in each were cattail-bulrush (25, or 42 per cent), sedge-bulrush (10, or 17 per cent), and sedge (10, or 17 per cent). Male blue-winged teal were rarely observed on waiting stations after the middle of June. The presence of a male on a waiting station during May and the

first half of June was used as an aid in locating the general area to search for a nest. Of 66 teal nests associated with male waiting stations, 41 were found by first locating the waiting male.

NEST SUCCESS

Three different cover types were examined for nesting blue-winged teal in 1949 (Table 3). Thirteen teal nests were found

TABLE 3.—FREQUENCY OF BLUE-WINGED TEAL NESTS LOCATED IN THE THREE COVER TYPES CENSUSED IN 1949

Cover Types	Acres	Number Nests Successful	Number Nests Unsuccessful	Totals
Bluegrass.....	1,611	30	102	132
Sedge-meadow ..	473	7	34	41
Hay fields.....	87	0	0	0
Totals.....	2,171	37	136	173

in bluegrass on Dewey's Pasture in 1948. Most of the cover available in the Ruthven Area for nesting was dominated by bluegrass. The sedge-meadow cover type formed a narrow band (Figure 9) around potholes

FIG. 9. Sedge-meadow cover formed a narrow band around the potholes and water areas.

and open-water areas. In such a typical growth form, it did not offer as extensive areas for nesting as did the bluegrass cover type (Figure 10). Hay fields, mostly alfalfa, timothy, or clover, were scarce in the habitat around the sloughs and lakes.

Only 3 (23.1 per cent) of 13 nests found in 1948 hatched successfully. In 1949, 37 (21.4 per cent) of 173 teal nests were

FIG. 10. A mixed stand of bluegrass nesting cover.

successful (Table 3). Of the 95 teal nests found around Barringer's Slough, 16 (17 per cent) were successful. This was the lowest percentage of hatched nests found on any of the four main study areas. A total of 14 of the 16 successful nests were located in bluegrass cover. At Smith's Slough, 6 of 31 nests hatched for a nest success percentage of 19.3. Nineteen of these nests were located in bluegrass and the other 12 were in sedge-meadow. The highest proportion of successful nests occurred in Dewey's Pasture where 10 (35.7 per cent) of 28 nests hatched. About 93 per cent of the nests found in Dewey's Pasture were located in bluegrass cover. In contrast to Dewey's Pasture, only 3 of 14 teal nests (21.4 per cent) were successful at Whitford's Slough. Of five teal nests located on several miscellaneous areas, two were successful and both occurred in sedge-meadow cover.

Some of the factors that might affect the nest success of the blue-winged teal were cover composition, fire, predation, grazing, parasitism, and human interference. The causes of nest losses in 1948 and 1949 are presented Table 4.

COVER COMPOSITION—Data in this study were obtained from 173 quadrats, 1/4,000 acre in size, located about nests. Ecological measurements made in an effort to determine the effects of cover on nest success included: height of cover around nest, light intensity at nest, amount of crown area controlled by the dominant cover plant, density of general cover surrounding nest, stem density of cover in the immediate vicinity of nest, topographic location of nest, and height of nest above the nearest

TABLE 4.—CAUSES OF NEST FAILURE IN 146 BLUE-WINGED TEAL NESTS ON THE STUDY AREAS IN THE RUTHVEN AREA DURING 1948 AND 1949

Destructive Agencies	Barringer's Slough	Smith's Slough	Dewey's Pasture	Whitford's Slough	Miscellaneous	Total
Skunks	25	4	13	5	..	47
Minks	14	3	2	..	..	19
Foxes	8	5	5	..	..	18
Raccoons	6	4	..	..	..	10
Weasels	..	4	..	..	..	4
Ground Squirrels	1	..	1	..	..	2
Cattle	1	..	1	..	1	3
Flooding	4	..	..	..	..	4
Mowing	1	..	..	..	..	1
Human	..	..	2	1	..	3
Undetermined	19	5	4	5	2	35
Totals	79	25	28	11	3	146

water level. Only light intensity and cover density were found to affect location and success of nests. (Tables 5 and 6).

TABLE 5.—SUCCESS OF BLUE-WINGED TEAL NESTS AS INFLUENCED BY AMOUNT OF LIGHT REACHING NESTS

	Per Cent Photo Reading					
	0–5	6–10	11–15	16–20	21–25	26+
Successful	10	14	8	2	2	1
Unsuccessful	27	43	30	13	14	9
Total Nests	37	57	38	15	16	10

TABLE 6.—SUCCESS OF BLUE-WINGED TEAL NESTS AS INFLUENCED BY STEM DENSITY OF THE COVER

	Stem Density (100 stems/sq.ft.)			
	Sparse 0–2	Light 3–4	Medium 5–6	Dense 7–12
Successful	26	23	14	7
Unsuccessful	101	77	63	20
Total Nests	127	100	77	27

Seventy per cent of successful nests were found in cover which could be arbitrarily classified as either sparse (0-299 stems per square foot) or light (300-499 stems per square foot). The light intensity at the nests and the stem density of the cover in the immediate vicinity were inversely proportional. Nests located in cover of light to sparse stem density with an overhead canopy producing a light intensity rating of less than 10 per cent apparently were more successful than those in the other covers utilized by nesting birds.

Since no teal nests were found in hay fields, analysis of the nesting data was concerned only with the bluegrass and sedge-meadow cover types. The sedge-meadow cover type (473 acres), for the most part, consisted of a complex intermixture of sedges, rushes, spike-rushes, mints, bur marigold, slough grass, cordgrass, bluejoint grass (*Calamagrostis canadensis*), and river grass (*Fluminea festucacea*). Water levels in this cover type varied from slightly moist soil to about 8 inches of water. On the upland, bluegrass was definitely the dominant plant. Other plants of the bluegrass cover type (1,611 acres) were the goldenrods, asters, vervain, greater and lesser ragweed, the tall and short bluestems, the grama grasses, wild rye, western wheatgrass, Indian grass, and the dropseed grasses.

A comparison of Bennett's (1938) nesting cover data with those obtained in this study strongly indicated that the availability of a particular cover type for nesting determined the probable frequency with which nests would be found in that cover.

FIRE—On April 20, 1948, about 70 acres of potential waterfowl nesting cover in the northwest corner of Dewey's Pasture burned. No duck nests were found in this area prior to the fire but about 5 weeks after the fire, three blue-winged teal nests were located in

the new vegetation. None of these was successful. Two fires in Dewey's Pasture in the spring of 1949 burned about 50 per cent of the available upland nesting cover. The earlier of these fires occurred on April 11 and covered about 10 acres in the southwest corner of the study area. The bluegrass made an amazing recovery from this early burn and, by the first week of June, the only apparent difference between this early-burned cover and the unburned cover was the lack of accumulated dead vegetation on the surface of the soil. Nevertheless, of six teal nests located in this general area, none was found in the burned portion. Two of the six nests were located within 3 to 5 feet of the edge of the early-burned cover. The lack of dead vegetation might have been sufficient cause for the females to nest elsewhere, for vegetation of a previous year's growth was utilized extensively in nest construction. The other fire in Dewey's Pasture in 1949 occurred on May 2 and burned the northern half of the area. A 2- to 3-week drought period occurred after this fire, and the vegetation apparently did not recover sufficiently during the summer to be attractive as nesting cover (Figure 11), for no duck

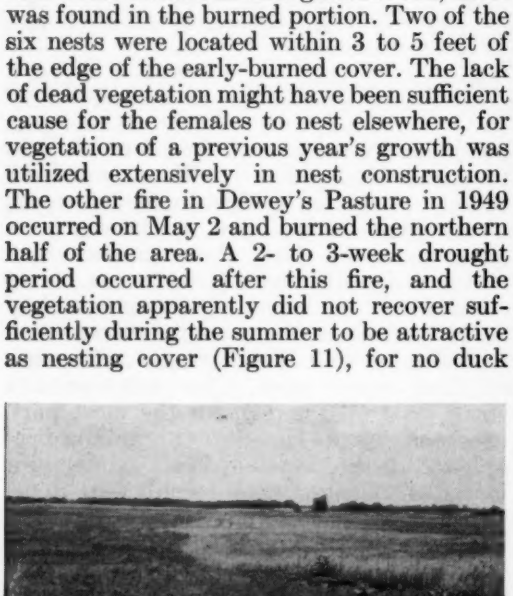


FIG. 11. Burned-over vegetation (left) was unattractive to nesting blue-winged teal.

nests were found. An area of about 4 acres burned on the west side of Barringer's Slough during the 1948 waterfowl hunting season. Intensive search in this fall-burned area did not yield a single duck nest, but in an adjacent unburned area separated from it only by an indefinite road, five nests were found. In 1949, in Dewey's Pasture, the burned cover of the northern half seemed sufficiently unattractive to cause the nesting population to shift and utilize the southern pond systems more intensively than in 1948. This example, coupled with data from Barringer's Slough, seemed to indicate that a concentrating effect resulted in nesting cover adjacent to a burned area.

PREDATION—A total of 123 (64.4 per cent) of 192 unsuccessful waterfowl nests was destroyed by animals preying upon the nest or incubating female (Figure 12).

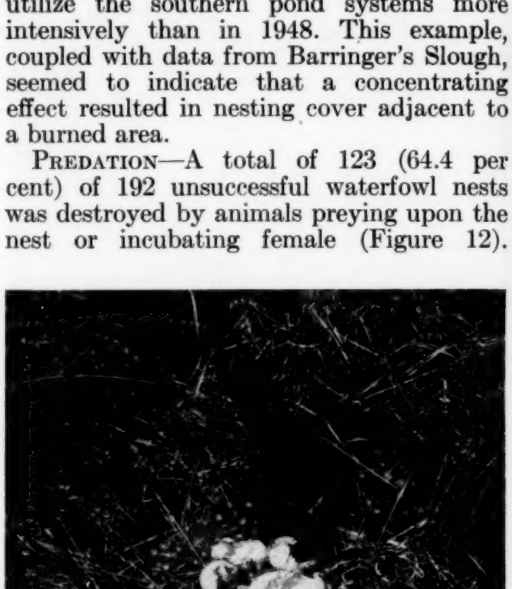


FIG. 12. Blue-winged teal nest in bluegrass destroyed by predation.

Destroyed nests attributed to striped skunks (*Mephitis hudsonica*) amounted to about 26 per cent, minks (*Mustela vison mink*) approximately 14 per cent, and raccoons (*Procyon l. lotor*) about 11 per cent. Predation was responsible for the loss of 100 of 186 teal nests under observation during 1948 and 1949.

Bennett (1938) stated that, among the fur-bearers, the striped skunk was surpassed in numbers only by the muskrat (*Ondatra zibethica cinnamomina*) in the Ruthven Area. This same condition pre-

vailed in 1948 and 1949 over the study areas except in Dewey's Pasture and Whitford's Slough. On these two areas, the striped skunk was by far the most abundant furbearer. Striped skunks were common also around the nesting margin of Barringer's Slough.

Mink were common on all the study areas. The heaviest population was believed to be present around Barringer's and Smith's Sloughs. The mink population apparently was increasing in the Ruthven Area, but the animals were not noticeably abundant in any one locality.

In 1948 there was one active red fox (*Vulpes regalis*) den in Dewey's Pasture, and in 1949 there were two. This did not indicate a population increase but rather a shifting of a family of foxes from Smith's Slough to Dewey's Pasture. An indefinite number of dens was present in the pastures surrounding the borders of all the study areas. In general, red foxes were sufficiently common to be observed during the day about once each week. Neither coyotes (*Canis latrans*) nor gray foxes (*Urocyon cinereoargenteus*) were encountered.

An abnormal increase in the raccoon population was noticed during both 1948 and 1949. Barringer's and Smith's Sloughs seemed to be particularly attractive to raccoons. The common appearance of raccoons in these two areas was noticeably reflected in the amount of nest destruction.

The long-tailed weasel (*Mustela longicauda*) was considered responsible for the destruction of four blue-winged teal nests in Smith's Slough in 1949. All of these nests were located within 100 yards of the weasel's den. Hansen (1947) reported that weasels were responsible for 9.5 per cent of the waterfowl nest destruction in Barringer's Slough in 1946.

It was difficult to determine the predator responsible for the destruction of any particular nest. Hansen (1947) discussed the inconsistency and impracticability of attempting to assess nest destruction to a particular predator. As with other investigators, the use of "sign" was employed in most cases to determine the predator. There were 13 cases in which at the first visit a complete clutch was recorded and at the second visit a week later, the nest was absolutely bare. Some of the "undetermined" nests were of this type but the greater portion of them would probably be attributable to mammalian predators. No avian predators were known to have been responsible for waterfowl nest losses.

Two particular locations in the nesting cover might be considered as "lethal areas" under Errington's (1936) classification. Not only were the nests regularly destroyed but in three instances the incubating females also were killed. The presence of an active mink den in one case and an inhabited fox den in the other were considered as the main factors responsible for the nest failures. A comparison of the ecological measurements of cover revealed no apparent difference between these particular nests and other nests located in similar cover.

GRAZING—Grazing was not permitted on the state-owned land of Dewey's Pasture but an adjoining area that was privately-owned and amounted to about 5 per cent of the environmental nesting unit was grazed. Smith's Slough was grazed sporadically by about six cattle during the early part of the 1948 nesting season. Cattle were not pastured there in 1949. About 40 per cent of the habitat suitable for duck nesting was grazed around Barringer's Slough, mostly on the west margin. Whitford's Slough was heavily grazed over approximately 90 per cent of its land area during the entire 1948 and 1949 duck nesting periods. Table 7 presents data on 173 blue-winged teal nests and their success in relation to the degree of grazing.

TABLE 7.—FREQUENCY OF 173 BLUE-WINGED TEAL NESTS IN RELATION TO THE DEGREE OF GRAZING AS WELL AS THEIR ULTIMATE FATE

Degree of Grazing	No. Nests Successful	No. Nests Unsuccessful	Per Cent Successful
Heavy (1 cow to 3 acres or less)	3	17	15.0
Moderate (1 cow to 4–6 acres)	1	17	5.5
Light to None (1 cow to 8 acres or more)	33	102	24.4

The nest success of blue-winged teal on Dewey's Pasture in 1948 was 23 per cent and

in 1949, 36 per cent. Comparative data were not available for previous years, but after a year of no grazing in Smith's Slough, 24 per cent of the teal nests hatched. In Whitford's Slough where heavy grazing had been permitted for many years, the nest success was approximately 21 per cent; however, the majority of the nests were located in isolated cover that was lightly grazed. About 402 acres of nesting cover around Twelve-mile Slough, a heavily grazed area, yielded only one blue-winged teal nest and two mallard nests after four intensive searches. Not one of the three nests was successful. Those areas which were classified as heavily grazed (Figure 13)

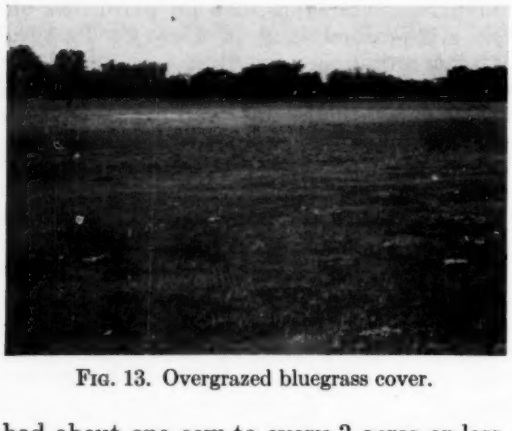


FIG. 13. Overgrazed bluegrass cover.

had about one cow to every 3 acres or less, while moderately grazed areas (Figure 14)

FIG. 14. Moderately grazed pothole margin (note nest marker in foreground).

had about one cow to 4 to 6 acres, and light to ungrazed areas supported one cow to 8 or more acres. Bennett (1937) conducted a grazing experiment on Dewey's Pasture and reported that it supported one duck nest per 9.3 acres when grazed at an intensity of one cow to 4.6 acres; when overgrazed, it supported no nests; and when left ungrazed, one duck nest per 11 acres. He concluded that the grazing of one cow per 6 acres in normal years appeared to be beneficial to duck nesting areas in Iowa. Hansen (1947) similarly reported that ungrazed and lightly grazed bluegrass and sedges were preferred as nesting cover by anatine ducks at Barringer's Slough. Considering the past studies and the data obtained from this investigation, it seemed reasonable to assume that more waterfowl would nest and a greater number of those nests would be successful if located in lightly grazed or ungrazed bluegrass and sedge-meadow areas.

PARASITISM—Only seven of 186 blue-winged teal nests were found that had been parasitized by the ring-necked pheasant (*Phasianus colchicus torquatus*). One teal nest at Barringer's Slough was parasitized by a shoveller (*Spatula clypeata*). None of the parasitized nests was successful, for they were either destroyed or deserted. All were found during the 1949 nesting season. Bennett (1938) reported that pheasant parasitism of duck nests was more prevalent during years of high pheasant populations. The pheasant population had been considered low during 1947 and 1948 but indications were that it had increased about 20 per cent in 1949 over 1948 in the areas utilized by nesting waterfowl. The data on hand tend to substantiate Bennett's hypothesis; however, it is not known whether a high nesting pheasant population is compatible or detrimental to waterfowl in duck-nesting habitat.

HUMAN INTERFERENCE — In 1948 one blue-winged teal nest was destroyed by bluegrass seed-stripping machinery. Another teal nest was deserted by the female after curious workmen visited the nest several times in one day. A teal nest in Whitford's Slough in 1949 apparently was deserted by the female after being flushed by the investigator. This was an unusual situation, for most of the females generally returned to their nests within a few hours. At Barringer's Slough in 1949, an incubating female was unintentionally stepped on by the investigator while searching dense nesting cover. Two of her eggs were broken.

The female flew about 30 yards and landed in dense vegetation. The damaged eggs were carefully removed from the nest and the cover returned to its original appearance as much as was humanly possible. A recheck on the nest a week later revealed that the female had successfully brought off a brood of ducklings. It is doubtful if flushing the ducks from the nests had a detrimental effect on the ultimate success. Of ten successful nests found in Dewey's Pasture in 1949, nine were located by flushing the female. At Whitford's Slough, two of the three successful nests were found by flushing the female.

RENESTING

Renesting attempts by blue-winged teal were determined in much the same manner as that used by Bennett (1938) and Hansen (1947). This included noting: number of eggs present, date of nest building, cover selected, amount of down in nest, and the relationship of a destroyed nest to a renesting attempt in the same territory. No attempt was made to differentiate between normal nests and renests among early small clutches that were destroyed. Females occasionally built and deposited eggs in as many as four different nests but data based on marked birds were not obtained. No instance was known of a female teal raising more than one brood a season.

At least 52 of 186 blue-winged teal nests were estimated to be renesting attempts. Fourteen (26 per cent) of these were successful. This is a higher degree of success than the 14.8 per cent reported by Bennett (1938) and lower than the 34 per cent given by Hansen (1947).

JUVENILE MORTALITY

Losses of young ducklings attributable to parasites and diseases apparently played a minor role in juvenile mortality, for no deaths from these factors were discernible.

One blue-winged teal juvenile was found that had been freshly killed and partly eaten by snapping turtles (*Chelydra s. serpentina*). Bennett (1938) considered the snapper as being scarce in the Ruthven Area during the period of his investigation. Evidently the aquatic environment on such areas as Barringer's Slough, Mud Lake, Smith's Slough, and Trumbull Lake was more favorable to the increase of this turtle than in Bennett's study, for as many as three to five snappers were observed daily during the periods of brood census in 1948 and 1949.

Minks were present in the study areas but an examination of fresh scats gathered at the dens during the 1948 waterfowl rearing season indicated that their depredations were mainly on the juvenile coots and pied-billed grebes (*Podilymbus podiceps*) rather than on ducklings.

No juvenile ducks were found in the vicinity where teal nests were known to have hatched. Blue-winged teal broods usually were observed first on the open water when they were about 2 weeks old, with an evident loss of two to three young per brood as compared to the mean number of eggs hatched (9.3) from normal nests in 1948 and 1949.

Counts were made of all broods observed throughout July and August each year. Many of the same broods were counted more than once, but distinction between broods previously counted and those observed on any one day was not possible. Nevertheless, a concerted effort was made to determine the number of distinct broods present on the different water areas on the basis of home range. Records of the brood counts made during the two years of study are shown in Table 8. There tended to be a slight recession from the time the broods were first observed to the beginning of the migratory stage.

TABLE 8.—MEAN BROOD SIZE FOR BLUE-WINGED TEAL IN RELATION TO AGE

Age in Weeks	Number Broods Counted	Brood Size per Female
2–3	20	6.15
4–5	18	5.66
6–7	14	5.71
8–10	12	5.16
Total	64	(42 considered distinct broods)

PRODUCTION

The yearly production for the Ruthven Area was determined by utilizing data obtained on nest densities, nest destruction, successful nests, and juvenile survival. In 1948 it was estimated that about 120 pairs

of blue-winged teal nested in the Ruthven Area. Since 23 per cent of the nests under observation were successful and the mean successful brood at the migratory stage was 5.8 juveniles, the calculated total number of blue-winged teal reared in 1948 was about 160 birds, with an average of 1.33 juveniles produced per breeding pair. Actual brood counts up to September 1, 1948, revealed that at least 93 juveniles were produced.

In 1949 the blue-winged teal nesting population was approximately 140 pairs. Since 21 per cent of the nests were successful and the mean successful brood size was 5.1 juveniles, the total number of teal reared was calculated to be about 189 birds, with the average number of juvenile teal produced per breeding pair being 1.35. Tabulation of distinct broods up to September 1, 1949, indicated that at least 123 juveniles were produced.

Bennett (1938) reported that each pair of blue-winged teal under his observation from 1932 to 1936 produced 3.09 young ducks to the migratory stage. Hansen (1947) estimated that the nesting population of 128 teal at Barringer's Slough in 1946 produced 2.02 juveniles per breeding pair.

MANAGEMENT

It seemed apparent from the survey of the nesting areas available to waterfowl in Iowa that a larger number of suitable nesting places were needed. Continued drainage of the small, but important, potholes and sloughs has left only a remnant of nesting habitat compared with that of 50 or even 15 years ago. The most important management practice for waterfowl in Iowa would be the acquisition and restoration of as much of the northwestern Iowa pothole country as is economically and financially possible.

Intensive environmental management for waterfowl alone can seldom be justified. With this in mind, it is necessary to utilize Nature's forces to the best advantage and recommend simple but practical land use practices. Since the data obtained in this study showed that pot-holes and small water areas were as important, proportionately speaking, as large lakes and sloughs, the following procedures are recommended to increase the utilization of these small areas by the blue-winged teal.

At present, cover located within a 150-yard margin of a small water area and having more than 75 per cent in grassy vegetation (bluegrass or sedge-meadow cover types) needs little more than continued protection from the detrimental effects of fire and overgrazing to be of value as nesting cover for land-nesting waterfowl. On areas where the grassy vegetation composes 50 to 75 per cent of the cover, two alternatives present themselves. First, if the grassy vegetation appears to be increasing in percentage composition, succession in this direction may be hastened by protection from fire and restriction against grazing until the cover is predominantly of a grassy nature. Spraying of noxious weeds and dense patches of forbs with herbicides will aid in the development of grassy cover. In the second alternative, where the grassy vegetation appears to be decreasing in percentage composition, removal of the herbaceous vegetation must be accomplished, followed by reseeding with bluegrass and the establishment of sod. Assuming that certain areas have been acquired that were formerly in cultivated crops, pasture, or hay crops, continuance of these areas in clover, alfalfa, or bluegrass is desirable.

Light grazing (one cow per 6 acres, or its equivalent in horses and sheep) can be permitted on nesting areas with little effect on the nesting population of ducks. After July 1, it might be satisfactory to permit light to moderate grazing of the marginal cover. A long-term cover crop plan, with good land management and water conservation practices, is necessary for maximum utilization of the area by waterfowl.

Reports by Moyle and Hotchkiss (1945), Hayden (1943), Provost (1947), and Bellrose (1941) have indicated that the alteration of water levels can bring about a profound change in aquatic plants. The judicious use of such a management tool could determine in part, the extent of the open water areas and the important "edge."

Artificial measures that transform certain parts or all of the cover ordinarily are not satisfactory for a long-term management plan. On strictly an experimental basis, it is recommended that the artificial creation of prominent objects along the shoreline to act as male waiting stations be tried in an effort to make more of the water areas attractive to breeding waterfowl. Descrip-

tions and the characteristics of male waiting stations have already been given in an effort to show what is utilized by breeding males.

Predator control in certain areas might affect the fall population and, as pointed out by Bump *et al.* (1947), may be useful in producing a greater fall surplus where such a crop is utilized for sport. A more feasible plan to control the fur-bearers that prey upon duck nests is to stimulate interest in trapping and the sale of fur. Education measures designed to interest and to teach the youth of the area the most effective means of catching minks, skunks, weasels, raccoons, and foxes might prove effective. Information leading to the handling of raw furs would be recognized as valuable to the trapper as well as to the fur industry.

Censuses are an important part of waterfowl management for they provide the waterfowl manager with data that will indicate trends within the duck population. The censuses employed in this investigation that might be of value to conduct periodically are: (1) spring migration count, (2) male waiting station count, (3) sample study area nest count, (4) summer brood count, and (5) fall migration count.

A delay of the waterfowl hunting season in Iowa to November 1, and correspondingly later further south, apparently would permit about 75 per cent of the blue-winged teal population to escape the heavy hunting pressure at the first of the season. Undue slaughter of teal during the peak of their fall migration might be eliminated by opening the season 10 days later than has been customary during the past three years

SUMMARY AND CONCLUSIONS

1. Four objectives were advanced in the proposed plans of this research: (a) to develop a method of determining yearly productivity prior to the hunting season, (b) to compare present with past productivity to determine waterfowl population trends, (c) to analyze some of the factors affecting waterfowl populations, and (d) to recommend management procedures for the marshes and sloughs of northwest Iowa to benefit nesting waterfowl.

2. The yearly production of waterfowl was obtained from data on nest densities, nest success, and brood counts.

3. From a series of censuses, the 1948 estimated breeding population of blue-winged teal in the research area was 120 pairs. In 1949 there was an increase in the breeding population to approximately 140 pairs.

4. Blue-winged teal nested from the first week of May to the first week of August, a period of about 100 days.

5. Nest sites were selected by the female teal and field observations on 63 females indicated that most of the nest building occurred from 7:00 to 10:00 a.m.

6. More than 80 per cent of the teal nests were constructed and lined with old bluegrass and down.

7. Blue-winged teal nests were found from 20 to 210 yards from open water, with the mean distance from open water for 186 nests being 79.4 yards.

8. Measurements taken on all nests indicated the following means: outside diameter, 7.7 inches ±0.56; inside diameter, 5.3 inches ±0.78; and bowl depth, 2.2 inches ±0.58.

9. Measurements of 142 teal eggs gave a mean width of 33.9 millimeters ±0.37 with a range from 30 to 37 millimeters, and a length of 47.1 millimeters ±0.75 with a range of 38 to 51 millimeters.

10. In 1948, 23.1 per cent of the teal nests hatched successfully and in 1949, 21.4 per cent.

11. The mean number of eggs hatched from 40 normal nests was 9.31.

12. Fifty-two of 186 nests were judged to be renesting attempts with 26 per cent hatching successfully.

13. In 1948 it was calculated that the number of juveniles produced per breeding pair was 1.33 and in 1949, 1.35.

14. Comparison of the 1948 and 1949 production data with those available on the same area in the past (1932-1936 and 1946), indicated a decline in the number of juveniles produced per breeding pair.

15. Some of the factors studied, which apparently affected nest success, were cover composition, fire, predation, grazing, parasitism, and human interference.

16. Nests located in cover of light to sparse stem density (0-499 stems per square foot) and light intensity ratings of less than 10 per cent were more successful than those in the other covers utilized by the nesting teal.

17. The detrimental effects of burning

were reflected in teal nesting populations as much as a year after the fire.

18. Predation was responsible for the loss of 100 of 186 blue-winged teal nests under observation. Striped skunks, minks, and raccoons were believed responsible for 51 per cent of the depredations.

19. Indications were that more waterfowl would nest and a greater number of those nests would be successful if located in cover that was lightly grazed or ungrazed.

20. Parasitism and human interference were minor factors affecting nest success.

21. Recommended management practices to benefit waterfowl nesting in Iowa include: (1) protecting a 150-yard margin of vegetation around water areas from overgrazing and fire, (2) spraying noxious weeds and dense patches of forbs with herbicides, (3) removing the plants where weedy vegetation dominates and reseeding with bluegrass, (4) maintaining present nesting areas, (5) educating youth of the area in trapping techniques and fur utilization, and (6) acquiring and restoring as much of the pothole country as is economically and financially possible by agencies interested in waterfowl conservation.

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TRAPPING TECHNIQUES FOR RUFFED GROUSE [1]

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Population research on ruffed grouse (*Bonasa umbellus*) has been handicapped in the past because it has been virtually impossible to live-trap adequate samples. Fundamental information on movement and longevity has been practically unknown for this species. To manage this important game bird intelligently a knowledge of its population dynamics is essential. Therefore effort was made in Wisconsin to develop effective live-trapping methods. This paper will describe the trapping techniques we are using currently for handling ruffed grouse in spring, fall and winter.

Much of the success in the development of effective trapping methods is the result of continual encouragement given to both authors by Cyril Kabat, Chief of Wildlife Research, Wisconsin Conservation Department. Donald R. Thompson of the Wisconsin Conservation Department assisted in the development of the technique for winter trapping in 1951. Frederick Holzer, Wisconsin Conservation Department, materially assisted the senior author in developing an effective fall trapping program.

Spring Trapping

Mirror traps have been used for trapping male ruffed grouse in both spring and fall for a number of years (Tanner and Bowers, 1948; Bendell and Fowle, 1950). Our mirror traps are built 12 inches high, 10 inches wide, and 23 inches long, since Mattison in this study found that the size of the trap described by Tanner and Bowers could be reduced to make the trap more portable. We used high-quality mirrors because a good image makes it easier to catch birds. Fish netting, rather than wire, enclosed both the top and sides, making the trap lighter and reducing injuries.

We recommend the following techniques to effect maximum captures with mirror traps:

1. Place the trap three to six feet from the spot where the bird drums. Placing it closer often frightens the bird.
2. Occasionally a wary bird will move and drum from a nearby log after the trap has been set. Hanging a white handkerchief over the new log will often frighten the bird back to where the trap is located.
3. After placing the trap on the log, walk to the spot from which the bird drums and look into the mirror to make sure the bird's image will be well centered.
4. Cover the trap on the sides and top with branches. This camouflages it for those grouse that are wary and, more important, helps prevent predation by hawks and owls.

We have found that these traps do not capture birds efficiently until the birds begin to drum regularly (April 15 to May 15 in Wisconsin). Rainy weather does not reduce the catch. Because birds are caught regularly in late afternoon, the traps should be run twice a day. Working with densities of 1 cock to 25 acres, we found that one man using about 8 traps could catch 10 to 20 birds per week during the active drumming period. This trap can, therefore, be an efficient tool for handling a large number of male ruffed grouse in spring.

Late Summer and Fall Trapping

The easiest time to trap large numbers of ruffed grouse is in August and September. At this time of year populations are close to their annual peak of abundance and are flocked as broods or portions of broods. We found cloverleaf traps with leads to be very effective in fall. The adaptation of this trap for ruffed grouse was suggested to us by Dr. P. F. English and William J. Bailey, Jr. of Pennsylvania State College. The design is almost identical to that used for capturing shorebirds by Low (1935).

Figure 1 shows the dimensions we found to be the most satisfactory. It is possible that the height of the central cage could be reduced somewhat. As this figure shows, the trap has four parts—a central cage, a

[1] A contribution from Pittman-Robertson Project W-13-R of the Wisconsin Conservation Department.

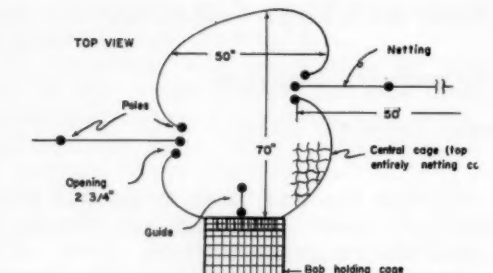

FIG. 1. Cloverleaf trap used to capture ruffed grouse in autumn.

holding cage, a guide, and netting leads. The netting leads direct the birds into the trap. The guide is needed to lead the birds into the holding cage as they walk around inside the central cage.

Figure 2 shows the construction details for two types of holding cages, a bob- and a ramp-cage. The bob-cage has willow poles on the side instead of fish netting because poles result in fewer head and wing abrasions. If burlap is stretched over the top of the bob-cage, head injuries are almost eliminated, since grouse will not attempt to fly against a solid top.

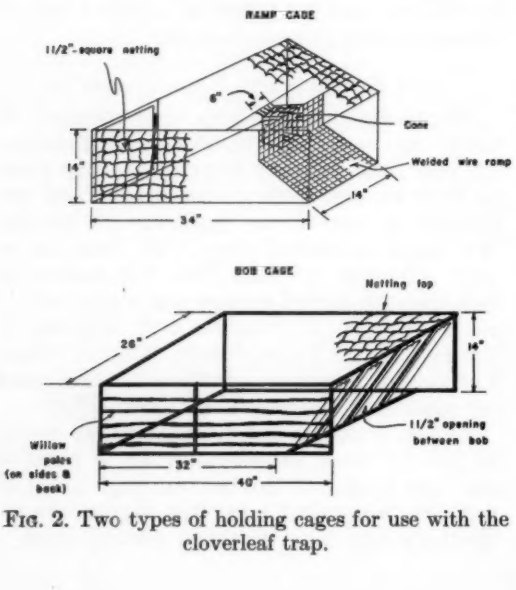

FIG. 2. Two types of holding cages for use with the cloverleaf trap.

The frame of the ramp-cage is made of soft wire. The birds walk up the ramp, through the cone and drop into the cage. The cone is needed to prevent birds from flying back into the central cage. Because the bob-cage is heavy, we only used it where it could be transported by car. When trapping away from roads, the ramp-cage is preferable because it can be collapsed and is light in weight.

Figure 3 shows the trap set upon bare ground.

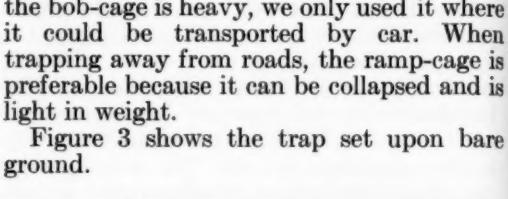

FIG. 3. Cloverleaf trap and holding cage set up on bare ground.

Since ruffed grouse may fly wildly about the cage when trapped, four daily visits to the traps are recommended to prevent exhaustion and injuries. Even though we visited our traps four times each day many birds were too exhausted to fly more than a few rods after release. The details for setting this trap are as follows:

1. Run netting leads flush with the V-shaped opening, or extend them about one inch inside the opening. This prevents birds from walking around the end of the netting without becoming entrapped.

2. Make the opening between the edge of the lead net and side of cage exactly 2-3/4 inches. This is narrow enough so birds have to squeeze a little to get inside. If the opening is made any larger, a good percentage of the birds are able to walk out in a few minutes.

3. Scrape away all sod and leaves under the holding pen so that mineral soil is exposed. Bare ground itself attracts ruffed

grouse and also makes bait more conspicuous.

4. Bait funnel openings and inside of central cage with berries grouse are eating in the wild. We found dogwood (*Cornus* sp.) berries, mountain ash (*Sorbus americana* and *S. Aucuparia*) berries, high-bush cranberries (*Viburnum trilobum*) and thornapples (*Crataegus* sp.) to be the most effective. On one trapping area dogwood was the number-one choice, while mountain ash was preferred on our other study area. Although these traps will catch birds without bait, we found that suitable bait would increase the catch about fourfold.

5. Place the leads at right angles to the direction the grouse usually travel.

6. Stake the central and holding cages to the ground to prevent the escape of trapped birds.

At our Rusk County trapping area we set traps about 60 feet back from the shoulder of a road with netting leads placed perpendicular to the road. In 16 trap days (September 15 to 30, 1953) Dorney and Holzer using 7 of these traps caught 86 ruffed grouse plus 24 recaptures. The excellent trapping success on this area was due to the high population attracted to the road edge for clover and other greens. These high roadside populations in September are quite common in many other heavily wooded areas of the Lake States.

Our other trapping area in Dunn County is in hilly country with farms in the valleys and woods on the hillsides. Ruffed grouse do not concentrate along roads here; this makes it more difficult to catch large numbers. Some of the highest populations occur in lightly grazed woodlots. By using lead nets only 12 inches high, Mattison was able to trap successfully in these grazed woodlots without undue interference from livestock. From August 4 to September 29, 1953 (42 trapping days), he caught 60 birds plus 9 recaptures with about 5 traps.

Cloverleaf traps are, therefore, a good method for handling ruffed grouse in August and September. This trapping technique makes it possible to handle broods during late summer for basic information on molt, survival, movements, and parasites. Grouse can be handled so easily it is now cheaper to trap than to collect them. Since these birds are banded just prior to the opening of the hunting season, the return of banded birds makes it possible to estimate the percentage of the population harvested by hunters.

WINTER TRAPPING

One of the first successful methods of catching ruffed grouse in winter was worked out by Mattison in 1951. The winter trap used is the wooden bob-cage shown in Figure 2 as a holding cage for the cloverleaf trap. The techniques found to be effective are as follows:

1. Build a shelter of leafy oak boughs and pine limbs in November and December. The shelter should be 3 feet square and 2 feet off the ground.

2. Clear all snow, leaves and sod from under the shelter.

3. Pre-bait the shelter with a mixture of dogwood berries, high-bush cranberries, soybeans (*Glycine Max*), and thornapples. We found dogwood berries to be most preferred.

4. When birds are regularly eating the bait, place the bob-trap under the shelter, leaving the bobs open so the birds can walk freely in and out of the trap. After grouse are accustomed to the trap, drop the bobs and begin the banding program.

This technique works well when the ground is covered with snow. In mild winters with bare ground, trapping is difficult. During the mild winter of 1952-53 Mattison caught 47 birds plus 91 recaptures from the middle of December to the first week in April. During the winter of 1953-54 which was milder than the preceding year, it was almost impossible to get birds to feed regularly under the shelters since bare ground was available throughout most of the winter. During a month and a half of trapping, only 16 birds plus 15 recaptures were handled. The entire cloverleaf trap, with boughs piled over it to provide shelter, was also given a short trial in the winter of 1953-54. It showed enough promise to warrant a more exhaustive trial in a normal winter.

The reason for the poor trapping in mild winters is that grouse have a greater variety of available foods than when the snow cover is deep, and hence are unwilling to take the bait live traps offer. They may also require less food. Their daily cruising radius is apparently reduced in warm weather, thereby decreasing the number of

birds to be caught at each trapping site. In our experience, winter trapping can only be highly successful when snow covers the ground.

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TRAPPING TECHNIQUES AND BANDING RETURNS FOR MICHIGAN SHARP-TAILED GROUSE [1]

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The problem of trapping various game birds and mammals to mark or band them for purposes of studying migration, emigration, longevity, and other phases of their ecology is an important consideration in the development of numerous research programs. In order to be of value to the ecologist in such studies, the animal must be captured, marked or banded, and released with the least possible injury. Each species, population, and sometimes individual, presents a new problem for which new techniques must be evolved. This has been the case in trapping gallinaceous birds. The clover leaf trap for ruffed grouse, the water lily trap and more recently narcosis-producing drugs for pheasants, the standard cock and hen trap for quail, the drop-net trap for turkey, and the tip top trap for sharp-tailed grouse are all techniques that have been developed to meet different circumstances.

This discussion will be limited to the techniques used for trapping sharp-tailed grouse, *Pediocetes phasianellus*, in the Upper Peninsula of Michigan, together with a brief summary of banding returns from sharptails banded and released in Michigan.

The first sharptails were trapped in Michigan in 1934, when 22 birds were taken in Baraga County and shipped to the Mason Game Farm to serve as a nucleus for a propagation experiment. After attempts to rear the birds in captivity failed, the state reverted to releasing live-trapped birds in suitable habitat throughout the Upper Peninsula and portions of the Lower Peninsula. Efforts to trap sharptails continued sporadically until 1951 when the present study was initiated and a more intensive trapping program was incorporated into the research activities.

WINTER TRAPPING

Four basic types of traps were used to capture sharptails from December until the first of April. These types, the tip top, long bob, portable funnel, and wing funnel, were described in a Game Bird Banding Manual compiled by Hawkins and Hamerstrom at the University of Wisconsin (1937). Such traps were in operation in the Upper Peninsula a total of 2,306 trap-days during the winters of 1951-52 and 1952-53. During that period, 58 different birds were handled a total of 144 times. All were males, 31 adults and 27 immatures.

The most successful trap used during the winter period was the tip top trap (Fig. 1). It was in operation a total of 1,881 trap-days, and succeeded in capturing 45 birds a total of 110 times. The advantages of this trap design over the others tested are as follows: trapped birds were protected from adverse weather conditions and possible predation; baits were off the ground and therefore free of snow; and drifting snow

[1] The data were collected as part of a research project sponsored by the Michigan Department of Conservation under the Pittman-Robertson program (Project 70-R). The study, initiated in July, 1951, and terminated three years later, was centered at the Cusino Wildlife Experiment Station, Shingleton, Michigan.

FIG. 1. The tip top trap.

usually did not affect the trap mechanism. The only major disadvantage was that alternate periods of freezing and thawing, or freezing sleet, would cause the edge of the trap door to freeze to the trap, rendering it inoperative. The weight of the traps and their bulkiness made them difficult to pack to areas inaccessible by road.

The long bob trap was built according to specifications, but later was modified as suggested by Newman (1951). This modification, *viz.*, that of adding another row of bob wires parallel but slightly offset to the original, proved to be a considerable improvement over the original design. Even with this extra row of bob wires, at least four birds escaped. Poultry mesh was used in the original construction, but this was later changed to cotton fish netting to prevent scalping. Even though the traps were placed on pieces of old snow fence to keep them out of the snow, high winds caused drifting snow to fill in behind the bob wires, and the traps would not operate. Another major disadvantage was that the trapped birds were exposed to the weather, and when the operator approached they would try to escape, often injuring a wing, and frequently scuffing the base of the upper mandible. Injuries occurred during these attempts to escape even though loose cotton netting was used to cover the trap. Although no sign of predation was noted during the trapping period of 1951-53, when the traps were operated 312 days and ten birds were handled 30 times, previous trappers in the Upper Peninsula reported two instances of predation on birds held in long bob traps. Four sharptails were killed in long bob traps; two by a snowy owl on December 22, 1949, and two by a rough-legged hawk on February 22, 1950 (Cusino Wildlife Experiment Station files). Under conditions of frequent deep snows, with high winds which occurred in the Upper Peninsula during the winter trapping periods of 1951–53, the long bob trap proved ineffective.

The effectiveness of the other two trap designs tested, *viz.*, the wing funnel, and portable funnel, was hampered by deep and drifting snow that clogged the funnels. The wing funnel trap was operated a total of 52 days and only two birds were caught. The portable funnel was in operation 61 days, and one bird was trapped.

The most effective of the four tested was the tip top trap. Hamerstrom (1942) reported that this trap, or slight variations of this design, was responsible for capturing 1,829 sharptails over a period of five years (1936-1941) in the Lake States region. A special material from which to construct the doors (metal doors may not freeze so readily) or a chemical to prevent the wooden doors from freezing shut would greatly improve the efficiency of this type of trap, and thus eliminate its only serious disadvantage.

The bait that was most consistently successful in attracting sharptails to the several types of traps used was the buds and catkins of white birch, *Betula alba papyrifera*. In all but one instance, when other baits were substituted trapping success declined. Trap-sites were pre-baited in early November with corn, mountain ash berries, and buckwheat. At only one location did the birds become accustomed to eating any of these baits. At this trap-site corn on the cob was readily taken from tip top and long bob traps. At six other locations corn and buckwheat were ignored. The mountain ash berries were eaten very sparingly, and because of the difficulty in keeping them out of the snow, and their limited quantity, they were not used during the major part of the trapping period. When the buds and catkins of yellow birch became available from commercial timber operations, they were substituted for the white birch which was more difficult to secure. Trapping success immediately declined, and there was

little evidence that the catkins were being eaten. White birch, a small amount of bog birch, and corn at one trap-site were used throughout the remainder of the trapping period. The areas in which the trap-sites were located did not support any type of agriculture, and it was not likely that the birds would come in contact with cultivated grains even during the winter periods when the flocks moved over greater distances. This factor probably was responsible for the limited trapping success.

All trap-sites were located on or within one-fourth mile of active dancing grounds. Several feeding areas were located and baited, but it seemed that the birds never remained in the baited areas long enough to become accustomed to the traps. As only natural baits were used, they were less attractive in areas where the birds were already feeding. After several unsuccessful attempts to trap birds in these feeding areas, the only trap-sites maintained were those on or near the dancing grounds where the males habitually came to loaf and display.

SPRING TRAPPING

The cannon-projected net trap was the most successful and economical technique for capturing sharp-tailed grouse in Michigan. This trap was first described in this country by Dill and Thornsberry (1950), for capturing waterfowl, but they suggested its possible use in the field of upland game bird management. Probably the first investigator to develop this trap for capturing upland game birds was Mr. H. G. Lumsden of the Ontario Department of Lands and Forests. He successfully used the net trap for capturing prairie chicken X sharptail hybrids in April, 1951. In May of that year, personnel of the Cusino Wildlife Experiment Station trapped five sharptails using a cannon net trap. Since that time, the net trap has been successful in capturing 79 different birds a total of 90 times. An average of five birds was captured each time the net was thrown. A maximum number of 11 birds was captured at one time (7 males and 4 females).

The original 50 by 25 foot net used in 1951 was replaced by a 100 by 60 foot nylon net in the spring of 1952. This two and one-half inch stretched mesh net was hung on a one-fourth inch manila rope. This mesh size proved a hindrance as the trapped birds could just push their heads through the mesh, and it was difficult to remove them from the net. A slightly smaller or larger mesh size would have been better. Four cannons were used to fire the projectiles which in turn propelled the net. In 1952 and 1953 the original Dill and Thornsberry type cannons were used with 15 grams of the potassium chlorate-sugar-blasting cap propellant. In the spring of 1954, the new Dill improved cannon assembly (Nelson, 1953) was used together with the recommended charge, and gave satisfactory results. The three-quarter inch manila rope spliced to the projectile was equipped with a large bull snap which served to connect it to the three ropes fastened to the net. In this way the projectiles could be disconnected from the net, and the net rolled for easier packing (Fig. 2). Standard army packboards were used to transport the trap into areas inaccessible by road (Fig. 3). The new Dill-type

FIG. 2. Snap and rings for connecting projectile to net.

FIG. 3. The cannon projected net trap packed for transport into areas inaccessible by road.

cannons and projectiles weighed 95 pounds packed, and the net approximately 55 pounds. Rubber covered light cord was used to connect the cannons, and provide a connection from the trap-site to the operator. No difficulty was encountered from rodent damage. A small ten-cap blasting machine was used to satisfactorily fire the cannons in 1952 and 1953, but two six-volt dry batteries seemed more effective in detonating the new cartridges designed for the Dill-type cannons.

Observations were made on all dancing grounds before trapping began to determine what portion of the display ground the birds were using. This increased trapping success, since the net could be set in the most advantageous position. The trap area was then cleared of any debris that would become entangled in the net either before or after firing. The net was usually set in mid-morning after it had been fired at another site. The end of the electric cord leading to the cannons was hidden in any convenient bit of cover which would hide the operator from the dancing birds the next morning. A vantage point was selected from which the observer could readily see both the operator and the area to be covered by the projected net. The observer and operator would take their places before dawn and await the arrival of the birds. When the observer saw that a maximum number of birds was within range of the net, he signaled the operator, and the net was fired (Fig. 4). The trapped birds were immediately covered with pieces of burlap to prevent further tangling, and they were removed from the mesh as quickly as possible.

The only injuries the birds suffered, other than the loss of a few feathers, was an occasional dislocation of the joint at the distal end of the tibia, and on one bird the humerus was broken. The disturbance

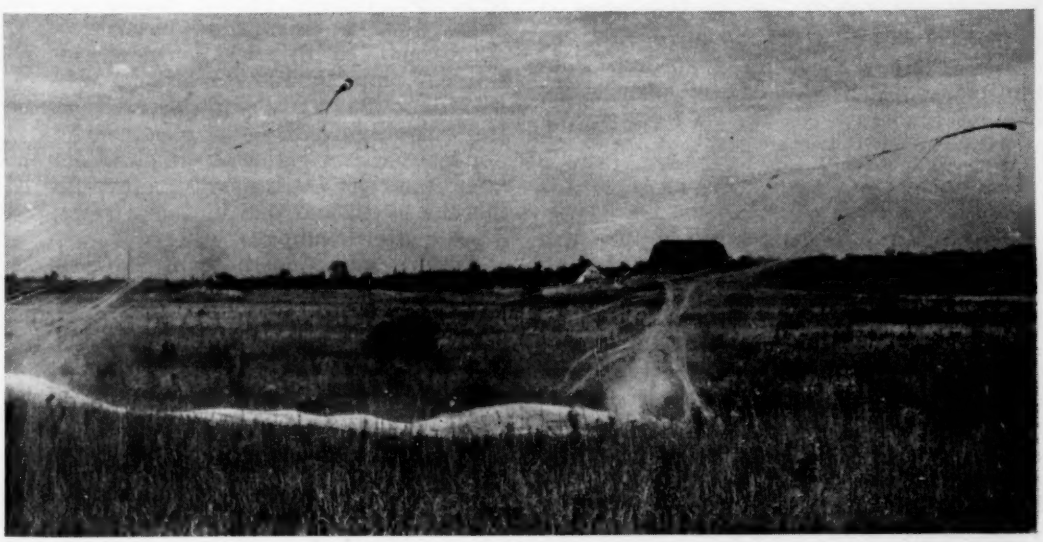

FIG. 4. The net trap immediately after firing. Angle of trajectory increased for photographic purposes.

caused by firing the net did not affect the dancing activity, since the birds returned to the dancing ground soon after the net was removed. The presence of the folded net on the dancing ground also did not hinder the activity, as birds were noted dancing on and across the net.

The costs involved in trapping upland game birds are usually very high, especially for those species or populations not accustomed to feeding on cultivated grain. The cannon net trap proved to be the most economical method tested for trapping sharptails. The net could be fired for approximately $12.00 including transportation, depreciation, and salary of the operator. Thus, for the three spring seasons the net trap was operated, the birds were trapped for between $2.00 and $3.00 each.

Difficulties were encountered in early spring, when freezing rain or snow would delay or prohibit trapping operations. Heavy frosts would tend to cause an uneven spread of the net even though the net was folded on a piece of muslin. The muslin strip was pegged down to prevent tangling by the wind. Occasionally one or more of the cannons would misfire, presumably due to a faulty connection, but these instances were kept at a minimum by using small plugs and sockets for automotive electrical systems, wrapping the connections in pliofilm, and inserting them in a piece of ordinary garden hose that had been cut on one side. It was found that the greater the electrical output of the detonating force the less chance there seemed for a misfire. Pliofilm covers placed over the muzzles of the cannons prevented the charges from getting wet during rainy weather.

SUMMARY OF BANDING RETURNS

A total of 117 sharp-tailed grouse was released at the trap-sites during the intensive trapping period of 1951 to 1954. Since the trapping techniques were highly selective as to males, especially adult males, most of the recoveries (70 per cent) were of that sex and age class. Fifty-five per cent of the birds released were not recovered again either by hunting or by further trapping operations. Of the birds recovered by trapping, 27 per cent were captured one to six months later at the point of release, 8 per cent were taken six months to one year later, 7 per cent one to one-and-one-half years later, and 3 per cent were retrapped one-and-one-half to two years later. All of these birds were recaptured at the point of release. Of the ten banded sharptails recovered from hunters, six were shot within one mile of the release site, and two birds were bagged within three miles of the trap-site. One bird was killed by a hunter 18 miles east of the trap-site nine months after it was released, representing the longest movement recorded for this recent investigation. One adult sharptail, trapped in late September, and released 20 miles west of the trap-site, was shot by a hunter within five miles of the trap-site (15 miles east of the release point) five days later. The number of returns from hunters is not indicative of gun pressure, since some of the birds were trapped and released on the Seney National Wildlife Refuge. Only two birds were retrapped at locations other than their original trap-site, and these only one-half mile from the original location.

Additional data regarding the movements of banded sharp-tailed grouse were available from recoveries on birds trapped and banded at various locations throughout the state from 1940 to 1954. Eighteen birds were recovered by subsequent trapping, 23 were taken by hunters, and one was found dead of unknown causes. All of the 18 birds (17 males and 1 female) which were retrapped a total of 30 times were captured within one-and-one-half miles of the original release point. Four of these birds were released approximately 18 miles southeast of the trap-site, but showed no homing instinct. All the other birds were released at the trap-site. Eight birds were retrapped within 6 months after banding; six, 6 to 12 months later; nine, 12 to 18 months later; one, 24 months later; and one bird was retrapped 3 years after banding.

Twenty-four banded sharptails (19 males and 5 females) were recovered either by hunting or in one case death from unknown causes. Sixteen (67 per cent) were reportedly shot within one mile of the trap and release site, four birds (17 per cent) within 1-3 miles of the release point, two (8 per cent) were shot within 3-5 miles, and no data are available regarding two band recoveries. Twenty-two of these birds (92 per cent) were recovered within 2 years following banding, one 2 years and 10 months later,

and one sharptail was shot 3 years and 10 months after banding.

The above data suggest that the Michigan sharptail is relatively sedentary in its habits. An individual bird probably never moves more than three miles from the nest-site during its lifetime. It must be emphasized that these movements are for a population which is not affected by the influence of cultivated grains. Since most of the data available are for male birds, which are probably of a more sedentary nature than the females, the suggested radius of three miles may be conservative. Migrant winter flocks, which it is felt are made up largely of females and immature males, were observed up to five miles from any known summer habitat during the intensive studies of 1951-53 in the Upper Peninsula. Recorded movements of some magnitude do occur, as was evidenced by the 15- and 18-mile recoveries observed during this study. Hale (1954) reported a movement of 54 miles for a Wisconsin sharp-tailed grouse.

SUMMARY

1. Four different types of traps were used to capture sharp-tailed grouse during the winters of 1951-52 and 1952-53 in the Upper Peninsula of Michigan. The tip top was found to be the most successful winter trap tested.
2. The buds and catkins of white birch were found to be the most successful bait. Trapping success declined when other baits were substituted.
3. The cannon-projected net trap was the most efficient method for trapping sharp-tailed grouse in Michigan. Description, modifications, and techniques used for net-trapping sharptails are given. Spring trapping seems preferable in that more areas are accessible both for releasing and trapping purposes. Spring releases in unpopulated areas may be more successful since the birds have a tendency to restrict their movements at that time. Better results (trapping more females) with the cannon net trap might be obtained where weather conditions are more likely to permit trapping throughout the peak of the dancing period.
4. A brief summary of banding returns from sharptails trapped and banded in Michigan from 1940 to 1954 is given, together with an interpretation of their significance.

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RELATIONSHIPS BETWEEN TEMPERATURE AND BLOOD OXYGEN IN THE LARGEMOUTH BASS[1]

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Studies of adaptations of various organisms to different factors of the environment are numerous; among these, environmental temperature in relation to poikilothermous animals has received considerable attention. It is generally agreed that for each organism and life stage, when all other factors remain constant, there will be an optimum range of temperature. The physiological responses of an organism to temperatures above and below this optimum range are stress responses and reflect the degree of lability or of adaptation in the physiological processes.

Lack (1945) stated that closely related species can rarely occupy the same habitat. In the process of competition between two similar species for comparable living conditions, one group will either become extinct or eventually occupy the peripheral areas of the same general habitat. The largemouth bass (*Micropterus salmoides*) and the smallmouth bass (*M. dolomieu*) appear to present such a pattern. The deeper, clearer, and colder areas of northern lakes and streams are dominated by the smallmouth bass, while the largemouth bass is found in the more shallow, weedy, and warmer bays. The successful existence of the largemouth bass in warmer, more stagnant areas can have resulted either from a true adaptation to these conditions or from a physiological lability that at times may have been taxed severely.

The purpose of this study was to ascertain certain relationships between water temperature and physiological response in the northern largemouth bass taken from a typical, shallow, thickly vegetated, northern lake.

During the summer of 1951, field tests were made of the oxygen content, pH, and temperature of several shallow-water areas in Lake Opinicon. At the same time largemouth bass were taken in hoop nets in these areas and tested for oxygen content of the branchial blood. By means of a hypodermic syringe, 0.25 cc. of blood was withdrawn from the branchial arteries. The blood was taken under oil with as little suction as possible. Whenever the blood was sucked, rather than pumped, into the syringe the sample was discarded. The syringe was then sealed with mercury and a small piece of rubber tubing with a glass plug. The whole apparatus was suspended in ice water in a thermos bottle for transportation to the laboratory. The oxygen content of the blood was analyzed by the Roughton-Scholander micro-gasometric apparatus (Roughton and Scholander, 1943). This apparatus can be well shaken to counteract the clotting effect of ferricyanide on blood. Two successive analyses were run on each sample. If the difference was greater than 0.5 volume per cent, the sample was discarded.

The oxygen content of the lake water was obtained by the Winkler method (Welch, 1948). The temperature was taken with a maximum-minimum field thermometer and the pH with a Beckman pH meter. Curran (personal communication) found only very minute quantities of carbon dioxide in Lake Opinicon during the day and, therefore, this factor was not measured although the importance of its effect on the respiration of fishes is recognized (Hoar, Black and Black, 1951).

During the following summer, studies were continued on the bass under controlled conditions. A tank, approximately 3 by 4 feet and 5 feet deep, was equipped with two heating units of 1000 and 500 watts to control water temperature. The latter unit was connected through a relay to a Fisher thermoregulator. An electric stirrer agitated the water, and air was bubbled through several stones from Thiberg aerators.

The pH of the lake water in the tank

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ranged from 8.0 to 8.4 during the experiment. The carbon dioxide content of the tank was not detectable by the usual alkaline titration method (Welch, *op. cit.*). The oxygen content of the water ranged from 3.5 to 6.0 cc. per liter, which is the usual range of oxygen in the lake during the summer, and was constantly renewed by the aerators.

In order to run tests at low temperatures, the tank was placed in a cold room where bass were tested at temperatures of 5 to 10° C. By means of the heating units the bass were tested at temperatures of 24 to 26, 32 to 33, and 35° C. At 35° C. the bass could be exposed for only one hour and were first placed in water at 29° C. for one-half hour so that the sudden change to a relatively high temperature would not kill them.

Each bass was suspended immobile, except for opercular movement, in a wire basket in the tank. A cloth over the eyes ensured quiescence. After two hours, a blood sample was taken by the method described. This blood was tested for oxygen content as described previously, for hemoglobin by the acid hematin method with a photo-electric colorimeter, for red cell number with a Levy counting chamber, and for lactic acid after the method of Barker and Summerson (1941). The oxygen capacity of 11 samples of blood at 5° C. was determined. The blood was placed in a flask and rotated in a cold water bath for 15 minutes and analyzed for oxygen.

The bass used in the tank were taken from lake water which ranged from 18 to 24° C. and may be considered to be acclimated to that particular temperature range. Groups of fish run at temperatures other than these were subject to temperature stress.

There is little relationship between the amount of oxygen in the bass blood and that in the lake water (Table 1). A minimum blood-oxygen load of approximately 5.7 cc. per liter was maintained regardless of the water oxygen and pH at these temperatures.

Data from the controlled tank are compared for the five temperature groups and have been plotted in Figure 1 according to the method of Dice and Leraas (1936). Twice the standard error of each mean is represented by the rectangles on either side of the center crossbar. When the total rectangular area on either side of the cross-

TABLE 1.—MEASUREMENT OF TEMPERATURE, pH, AND DISSOLVED OXYGEN (CC. PER LITER) IN LAKE WATER AND THE CONCENTRATION OF OXYGEN IN THE BRANCHIAL BLOOD OF THE LARGEMOUTH BASS

Temperature (°C)	pH	Oxygen in Water	Oxygen in Blood
21.5–22.0	7.4–8.3	2.80–5.40	5.85–23.45
22.7	6.9–8.3	2.86–6.76	5.72–28.75
23.0	7.3–7.5	2.86–3.55	5.70–17.72
23.3–24.0	8.2–8.5	5.30–6.42	5.85–23.00
25.0	8.4	6.35–6.38	5.72–17.19

bar of one group does not overlap that of another group, the means are significantly different. The blood-water oxygen ratios are not significantly different among the various groups, but at low temperatures (5 to 10°C.), an average opercular pulse rate of 16 per minute was sufficient to load the hemoglobin with as much oxygen as can be loaded at higher temperatures with a five-fold increase in opercular rate.

The differences in hemoglobin values from the branchial blood of the various groups are represented in Figure 2 by the same

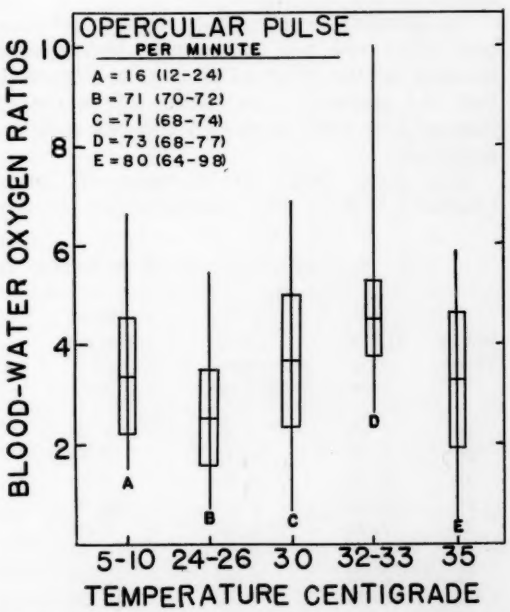

FIG. 1. The ranges, means, and standard errors of the blood-water oxygen ratios of the five groups of largemouth bass at various temperatures.

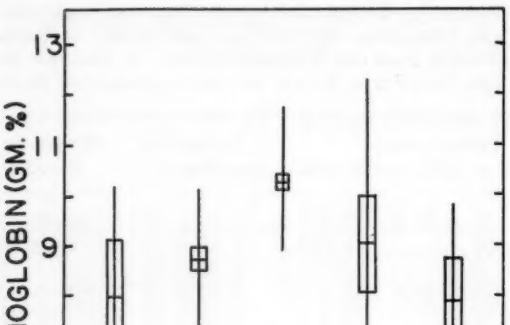

FIG. 2. The ranges, means, and standard errors of the hemoglobin values of the five groups of fish at various temperatures.

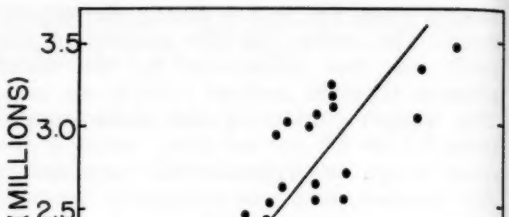

FIG. 3. The relation of hemoglobin and red-cell count of all the experimental fish regardless of water temperature.

method used for Figure 1. The amounts of hemoglobin in Groups C and D are greater than in the other groups, and the mean for Group C is significantly different from the means of the other groups.

A variable relationship exists between individual red cell count and hemoglobin content of the cells as shown in Figure 3, but the general relationship of increased hemoglobin with increased red-cell number is obvious.

The data from 11 samples of blood (Table 2) show the relationships among red-cell count, hemoglobin, oxygen load, oxygen capacity, and lactic acid content. No correction was made for the consumption of oxygen by these nucleated erythrocytes but the tests were run immediately after withdrawal. The amount of oxygen carried by the blood at any of the experimental temperatures was far less than the capacity of the blood.

In these experiments, the number of erythrocytes (Table 3) varied from 1,720,000 to 3,480,000 cells per militer, the hemoglobin from 5.52 to 12.30 grams per 100 milliliters, the blood oxygen from 1.90 to 48.80 cc. per liter, the oxygen capacity from 42.00 to 86.40 cc. per liter, and the lactic acid from 28.35 to 270 milligrams per cent.

TABLE 3.—COMPARISON OF OXYGEN CAPACITY OF BLOOD AND RELATED FACTORS

Water Temp. °C	Gill R.B.C. (millions)	Hemoglobin (gm./100 ml.)	Blood Oxygen (cc./liter)	Oxygen Capacity (cc./liter)	Oxygen Capacity (1 gm.Hb = 1.34 cc.O_2)	% Loss HbO_2	Lactic Acid (mgm. %)
10....	1.72	5.52	11.70	49.50	73.96	32.90	96.00
26....	1.77	6.42	3.70	50.02	86.02	41.80	68.35
35....	2.47	6.50	9.90	53.20	87.30	39.91	64.56
26....	2.72	7.16	22.70	47.20	95.94	50.70	32.04
35....	2.21	7.30	1.90	42.00	97.70	57.10	29.04
35....	2.36	8.20	16.90	59.30	109.90	46.00	78.26
32....	2.52	8.53	12.80	66.50	114.13	41.70	64.78
32....	2.93	8.76	12.60	77.00	117.60	34.50	141.36
24....	2.20	9.58	25.20	80.10	128.37	37.60	74.88
35....	2.85	9.75	13.50	86.40	130.90	34.00	114.80
32....	3.24	9.85	11.50	72.60	131.90	44.80	76.20

TABLE 2.—MEASUREMENT OF OPERCULAR RATE, OF HEMOGLOBIN, RED-CELL NUMBER, OXYGEN CONCENTRATION AND LACTIC ACID OF BRANCHIAL BLOOD FROM FISH OF KNOWN SEX AND WEIGHT AT VARIOUS WATER TEMPERATURES

Sex	Weight (oz.)	Opercular Rate/min.	Hemoglobin (gm./100ml)	Red Cells (million)	Blood Oxygen (cc./liter)	Lactic Acid (mg. %)	Temperature °C
M.....	26	12	8.92	2.61	29.10	157.50	5–10
M.....	23	12	7.70	3.35	12.80	170.50	
M.....	12	14	8.30	2.25	19.60	28.35	
M.....	24	22	7.22	2.15	34.60	47.88	
F.....	16	18	8.35	2.13	48.80	66.60	
F.....	54	16	10.15	3.19	22.50	32.73	
F.....	20	24	5.52	1.72	11.70	96.00	
M.....	24	70	7.15	2.00	4.90	81.70	24–26
M.....	40	71	9.25	1.81	19.70	78.00	
M.....	40	70	8.50	2.42	4.90	141.00	
M.....	28	72	9.50	2.65	14.70	234.00	
M.....	24	70	9.58	2.20	25.20	74.88	
F.....	28	72	9.90	3.12	19.60	97.80	
F.....	24	72	10.10	2.70	15.80	138.00	
F.....	42	72	9.60	2.25	19.30	168.00	
F.....	22	70	8.05	2.46	16.70	270.00	
F.....	76	71	6.42	1.77	3.70	261.00	
F.....	29	72	7.16	2.72	22.70	32.04	
M.....	30	72	8.85	2.62	19.50	63.60	30
M.....	22	74	11.75	3.34	12.60	93.80	
M.....	18	72	10.00	2.55	2.80	104.70	
M.....	16	70	9.00	....	28.20	216.40	
F.....	30	70	11.70	3.02	16.80	128.40	
F.....	32	68	9.50	2.55	17.10	64.56	
M.....	20	72	12.30	3.48	11.60	.....	32–33
M.....	12	74	8.93	3.04	26.00	.....	
M.....	32	72	8.53	2.52	12.80	64.78	
M.....	16	68	8.76	2.93	12.60	141.36	
M.....	12	76	9.41	3.00	31.80	58.08	
M.....	12	72	9.85	3.24	11.50	76.20	
M.....	28	70	7.71	2.01	29.50	116.40	
F.....	17	74	6.95	2.01	14.00	.....	
F.....	22	77	8.81	2.32	26.80	44.52	
M.....	32	80	9.75	2.85	13.50	114.80	35
M.....	12	98	7.30	2.21	1.90	29.04	
M.....	48	90	7.80	2.35	20.00	.....	
M.....	9	85	6.65	3.15	24.60	.....	
F.....	40	64	8.85	3.36	22.30	100.08	
F.....	20	80	8.20	2.36	16.90	78.26	
F.....	36	72	6.50	2.47	9.90	64.56	

At high temperatures, the relationship between weight of fish and lactic acid content of the blood was variable (Fig. 4). At low temperatures this relationship appears to be more consistent due to the counteracting influences of loading at the gills and discharging at the tissues. High *in vivo* temperatures (30 to 35°C.) do not appear to reduce consistently the combining power of hemoglobin in bass blood with oxygen (Fig. 5). Increased levels of lactic acid accompanied an increased combining power of the bass blood at various levels of hemoglobin (Fig. 6).

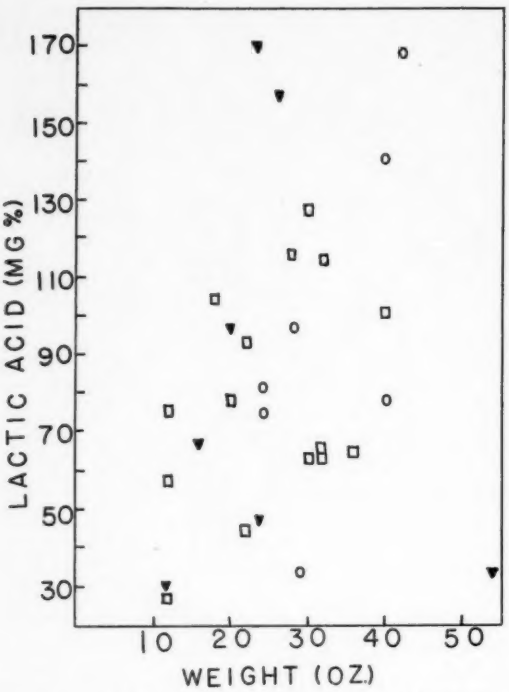

FIG. 4. Weight of the experimental fish plotted against individual lactic acid levels according to temperature groups, ▼ 5–10°C.; ○ 24–26°C.; □ 30–35°C.

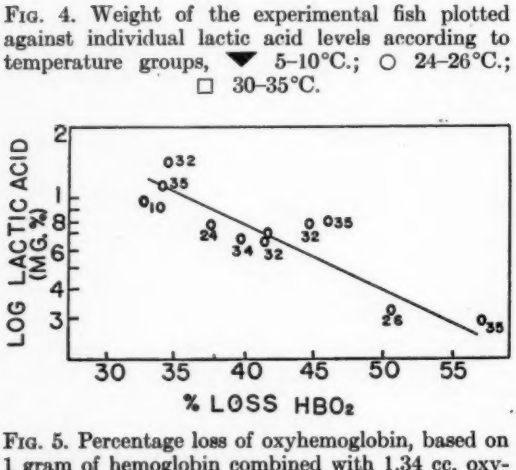

FIG. 5. Percentage loss of oxyhemoglobin, based on 1 gram of hemoglobin combined with 1.34 cc. oxygen, plotted against the lactic acid level of 11 samples of blood as taken from the fish at various temperatures.

THE RELATIONSHIP BETWEEN WATER TEMPERATURES AND BLOOD OXYGEN—Although the temperature range of the lake water in the field experiment was not large, it is clear that there is little direct relation between oxygen content of the water and that of the branchial blood of the bass. The results from the tank fish also revealed a

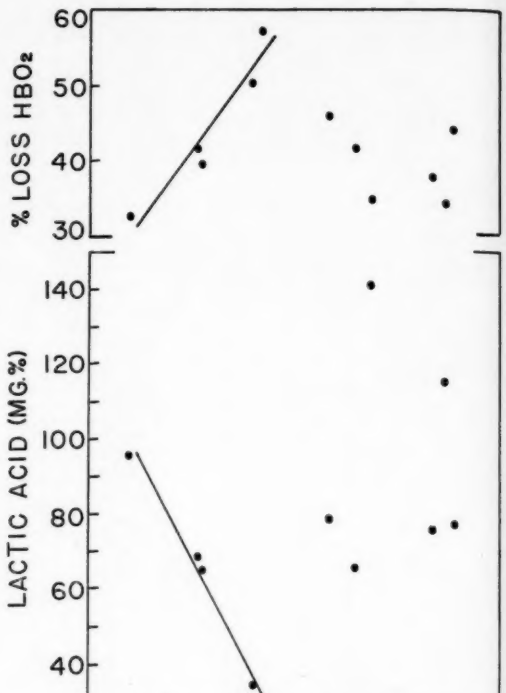

FIG. 6. Percentage loss of oxyhemoglobin and lactic acid values plotted separately against the hemoglobin values of 11 samples of blood.

lack of direct relation between water oxygen and blood oxygen. The loading of oxygen is simply facilitated at low temperatures without much effort on the part of the fish. At low temperatures the opercular rate is very slow and the resulting blood oxygen level is approximately that of fish at much higher temperatures when the opercular rate is higher. An increase in the oxygen of venous blood of the blue catfish, *Ictalurus punctatus*, but not of the carp, *Cyprinus carpio*, with increased oxygen content of the water was found by Powers *et al.* (1932), but these results were obtained over a wide range of oxygen values for the water.

The largemouth bass of Lake Opinicon can obtain sufficient oxygen at water oxygen values as low as 3 cc. per liter at temperatures below 30°C. The blood oxygen is maintained so that it rarely drops below 5 cc. per liter. Winterstein (1908) found that several kinds of freshwater fish could

live successfully in water containing only 0.6 cc. of oxygen per liter at 15°C. During the summer these largemouth bass would seldom be subjected to such a low oxygen content in Lake Opinicon where photosynthesis is high. It is likely, however, that during the winter they cope with low oxygen which is readily loaded because of the low temperatures. The noted absence of the largemouth bass in the shallow areas during the hot weeks of August is reasonably explained on the basis of plant respiration at night, with the carbon dioxide as well as the high temperature interfering with the oxygen loading.

It has been previously shown by a number of investigators including Barcroft (1914), Kawamoto (1929), and Irving, Black, and Safford (1941), that the amount of oxygen taken by hemoglobin varies inversely with the temperature. The critical temperature for the largemouth bass from Lake Opinicon is 30°C. At this temperature certain obvious physiological changes occur; the opercular rate is high (Fig. 1) and there is an increase in the hemoglobin of the branchial blood (Fig. 2). At cold temperatures of 5 to 10°C. the opercular effort is small, there is no increase in hemoglobin of the branchial blood, and loading at the gills is facilitated by the low temperatures.

Hall (1928) found that asphixia caused hemoconcentration in menhaden, *Brevoortia tyrannus*, and puffer fish, *Spheroides maculatus*, thus giving an apparent increase in the iron content of the blood. The spleen was constricted and apparently a true increase in circulating iron may also have occurred. Westfall (1943) demonstrated an accumulation of red cells in the gill arteries of goldfish, *Carassius auratus*, under anoxic conditions and a decrease in specific gravity of the blood of the general circulation. In this present experiment with largemouth bass, no significant difference in the specific gravity of plasma was obtained by the falling-drop apparatus in comparisons between the branchial blood of bass maintained at 24 to 26°C. and those at 32 to 35°C.

If it may be assumed that during the field tests the values of oxygen found in the branchial blood of certain of the largemouth bass at least roughly reveal the minimum amount of oxygen required (5.5 cc. per liter), then the tank fish would not seem to be suffering from asphixia during the experimental period. The mobilization of the red cells at the gills would be a direct result of temperature and not of oxygen lack. As Redfield (1933) pointed out, however, the true picture of respiration is the compromise attained between loading of hemoglobin at the gills and the discharge of oxygen at the tissues. If the red cell count of the general circulation is lowered at the expense of accumulation in the gills, then the tissues may be suffering anoxia. The surface properties of red cells can be altered by temperature and acidity and this may account for the accumulation in the gills. This increase in red cells will occur either directly from general anoxia as demonstrated by Westfall (*op. cit.*) or through increased body temperature.

LACTIC ACID—During and following exercise, the lactic acid level of the blood generally rises. Secondat and Diaz (1942) measured the level of lactic acid in the blood before and after exercise in two species of freshwater fish and found a range of 13 to 18 milligrams per cent before exercise which is comparable to that of man and of dog at rest. Immediately after exercise, the levels rose to a range of 33 to 79.5 milligrams per cent. In most individuals, the level fell in six hours, except for a few fish that died at increased levels of 112.8 to 155 milligrams per cent. Auvergnat and Secondat (1942) found that after exercise the pH fell in correspondence with the increased lactic acid level and that the carbon dioxide level was greatly reduced for purposes of buffering. This buffering action was slow in comparison to that of mammals.

The bass in the present study were tested for lactic acid after a quiescent period of two hours in the experimental tank. These lactic acid levels, except for any increase due to a short, initial struggle, are largely a result of temperature on metabolism. Many of the bass had lactic acid levels over 100 milligrams per cent and several over 200. The high lactic acid levels were sometimes accompanied by low oxygen tension in the gills. While high temperature inhibits loading of oxygen at the gills, it also facilitates discharge at the tissues, as does a slight increase in acidity. It appears that there are great individual variations in these bass as regards the balance between loading and

discharge of oxygen. Two possible explanations might relate to size and to the efficiency of utilization of oxygen from the swim bladder. When the weight of the fish from the various temperature groups is plotted against lactic acid (Fig. 4), the general relationship is one in which the larger fish produce the greater amounts of lactic acid. The trends within different groups at the higher temperatures are inconsistent. Under conditions of quiescence at cold temperatures any trend between size of fish and lactic acid level should be minimized by the balance of excellent loading at the gills, equalized red cell numbers between gills and general circulation, and low metabolism against retarded discharge of oxygen at the tissues as indicated by the present data (Fig. 4).

Unfortunately, no information on the swim bladder was obtained in this study. A few of the bass tested at 30 and 35°C. were returned to the retaining tank (18 to 22°C.) for observation. These fish always had great difficulty in maintaining an upright position and would float at the surface.

A progressive relationship between hemoglobin and oxygen capacity in the bass is indicated by the data in Table 3. The amount of oxygen taken up by these samples of blood is far less than the hemoglobin levels would suggest. If one gram of hemoglobin combined with 1.34 cc. of oxygen, which is the approximate value for vertebrates, there would be roughly twice as much oxygen taken as was actually measured. Low oxygen capacity and great variability in fish blood has been noted (Root, 1931; Redfield, *op. cit.*), but has not been adequately explained.

Root (*op. cit.*) added increments of lactic acid to sea robin, *Prionotus carolinus*, blood and equilibrated the blood at an oxygen pressure of 153 millimeters of mercury. He demonstrated that the percentage loss of oxyhemoglobin in relation to potential capacity increased with the rising levels of lactic acid in blood samples with the same hemoglobin values. The relation between lactic acid and percentage loss of oxyhemoglobin in largemouth bass is somewhat different (Fig. 5). The bass with various hemoglobin values have oxyhemoglobin losses of 30 to 60 per cent when lactic acid is present in quantities from 150 to 25 milligrams per cent respectively. This is an inverse relation, and the combining power of the blood is better at increased lactic acid levels. Irving, Black, and Safford (*op. cit.*) found with trout (*Salvelinus fontinalis*, *Trutta trutta*, and *T. irridea*) that the oxygen capacity of the blood was lowered permanently after an hour at 30°C. and after a very short time at 35°C. *in vitro*. The temperatures of the fish from which the blood was taken are shown in Figure 5. Blood from fish at 32 and 35°C. gave percentage losses from 34 to 57, and blood from fish at 24 to 26°C. had losses from 37 to 50 per cent. Although this is not comparable to a series of tests at different temperatures on portions of one sample of blood, it does indicate that high temperatures *in vivo* have not had a consistent effect on the oxygen capacity.

In order to ascertain other possible influences on the oxygen capacities of the bass blood, percentage loss of oxyhemoglobin was plotted against hemoglobin and lactic acid against hemoglobin (Fig. 6). The trends of these data break at hemoglobin values between 7.30 and 8.20 grams per 100 milliliters of whole blood. The data to the left and the right of the break can be designated as Group A and Group B, respectively. In Group A, the lower hemoglobin values were accompanied by the higher lactic acid levels and gave a lower percentage loss of oxyhemoglobin. In the same group, blood with higher hemoglobin values had lower lactic acid levels and there was a high percentage loss of oxyhemoglobin. The trends for the data in group B are not as clear, but certain relationships are evident. In general, the percentage loss of oxyhemoglobin is less as the hemoglobin value increases. By comparing the data point for point in Group B, it is seen that the higher the lactic acid the lower the percentage loss of oxyhemoglobin. The sharp break in the data indicates that some mechanism operates at low hemoglobin values to increasingly improve oxygen combination in the presence of rising lactic acid levels. At the higher values of hemoglobin this mechanism is less effective. It is not within the scope of this study to reveal the mechanism.

At 30°C., when the red cells accumulate in the gills, this increased combining power of the blood in the presence of high lactic acid does not mean that the oxygen supply

to the general body tissues is improved. At temperatures somewhat below 30°C., where accumulation of red cells in the gills is not great, there may be considerable advantage to this increased combining power and it might be considered an adaptation.

Hart (1945) demonstrated that the largemouth bass of Florida is very sensitive to carbon dioxide, has a low mean stroke output, and a high diastolic blood pressure compared with catfish and bullheads. From the present study, it appears that the northern largemouth bass has considerable tolerance for lactic acid. A high percentage loss of oxyhemoglobin is more directly related to low lactic acid levels than to the possible effect of high temperature on the blood *in vivo*.

The environment of the northern largemouth bass is that of warm, thickly vegetated, shallow lakes or bays. As the temperature of these areas increases the bass either seek deeper water, as in Lake Opeongo (Hart, *op. cit.*), or remain quietly in the shade of overhanging trees along rocky shores or under masses of water lilies, as observed in Lake Opinicon. During this quiet period of several weeks in August, their stomachs are empty and they are difficult to catch by line and bait. At this time the northern largemouth bass reveal that they have reached a state close to their physiological limit. At these high temperatures (28 to 30°C.) loading at the gills is difficult and the compensatory high blood pressure is probably reduced by vasodilation. An increase in the combining power of the blood through rising lactic acid levels at the expense of reduced carbon dioxide (Auvergnat and Secondat, *op. cit*), and the reduced metabolism through quiescence and starvation help to maintain a precarious existence. By extending physiological lability to its limit during part of the year the largemouth bass has been able to occupy the more rigorous habitats of the northern lakes.

SUMMARY

Measures of physiological response of northern largemouth bass to various temperatures were taken to ascertain the degree of adaptation of the bass to its environment. These measures include hemoglobin, red-cell count, arterial blood oxygen, oxygen capacity, and lactic acid.

The amount of arterial blood oxygen is more closely related to water temperatures than to oxygen content of the water. At high body temperatures during quiescence, hemoglobin increases in the gills, the opercular pulse rate increases, and the lactic acid level rises considerably.

In blood taken from bass at various temperatures, increased lactic acid improves the combining power of hemoglobin with oxygen. Percentage loss of oxyhemoglobin is more directly related to lactic acid level than to the possible destructive effect of high temperatures on the hemoglobin *in vivo*.

The northern largemouth bass appears to occupy certain habitats through physiological lability rather than through direct adaptation.

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SAMPLE SIZE IN FOOD-HABITS ANALYSES [1]

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INTRODUCTION

The number of stomachs which must be analyzed to establish the food habits of a population is frequently a perplexing problem. Methods which have been found useful for answering this question are herein discussed. In most cases, well-known statistical principles are applied to food-habits studies. The animals in the sample must, therefore, be collected at random in order to have the methods apply.

Certain terms are used in the following way. The size of sample means the number of animal crops, rumens, or other organs of the digestive system which are examined for food contents, and all of these organs will generally be referred to as stomachs. The term population is used here only in the ecological sense. Major foods mean those foods eaten in greatest amounts by either volume, weight, or frequency. The decision as to what are major foods will have to be decided arbitrarily by each worker.

Davison (1940) noted how increase of sample size changed the relative volumes of different foods eaten by bobwhite. When relative volumes changed less than a very few per cent, he considered the sample adequate. Korschgen (1948) noted how enlargement of cumulative totals of bobwhite crops added kinds of food not previously encountered. He considered a sample adequate when a cumulative total of crops contained enough kinds of food so that these kinds made up about 99 per cent of the volume previously found in all the crops.

In general, the more homogeneous the universe studied, the smaller the sample need be. A more homogeneous universe should result if the animals are collected from only one ecologic population during one season. Obviously, the food habits of a species may vary from community to community and from time to time. Therefore, the sample needed from one population during a certain season may not be the same as from a different population and/or a different season.

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PROPORTION OF ANIMALS EATING ONE FOOD

The number of stomachs which must be examined to ensure desired accuracy when investigating the proportion of a population which eats one certain food can be determined in the following way. Let p equal the proportion of the animals of a population which has the given food in their stomachs and let it be assumed that p remains constant during a certain season.

If, by some magical device, the contents of the stomach of each living animal of the population could be perused, p would be known. Since no such device exists, a few stomachs must be examined in the hope of getting a good estimate of that value.

Each investigator must decide the accuracy he wishes in his estimates. For example, he might want to be sure that the sample estimate of p is within 6 per cent of the true value. Thus, if the estimate of p is 33 per cent, he wants to be sure that the actual value is between 27 and 39 per cent. Unfortunately, there is no way to be absolutely sure that p lies within this range unless every animal in the population is examined. But the confidence that the estimate is within the above limits can be measured. For example, he can be confident that p is included in the given limits 95 per cent of the time.

The sample size can be estimated from the following equation (Cochran, 1953: 50-59)

$$[1] \quad N = \frac{4p\,(100-p)}{d^2}$$

where N equals sample size, and d equals permissible deviation from the true value of p. Although p is not known exactly, some value must be given for it in order to compute N. It may be known from a previous study that p was a certain amount, or that p varied between certain limits, say 60 to 90 per cent. In the latter case, where it is known that p will likely fall between certain limits, the limit closest to 50 per cent can be selected and used for p in the formula. But if no previous information about the proportion is present, a small number of stomachs could be collected in order to get an estimate of p to use in Formula [1].

Sperry (1941) found that 51 per cent of 319 coyote stomachs collected in April contained rabbits. In order to determine the status of rabbits as coyote food in April of a future year but in the same region, Sperry's value of p can be used. The number of coyotes which must be collected in order to be 95 per cent confident that the sample p (of rabbits) will be within 3 per cent of the true value can be estimated. Substituting in [1] $p=51$ per cent, and $d=3$ per cent, it is found that

$$N = \frac{4\text{x}(51)\text{ x }(49)}{(3)^2} = ca\ 1111$$

Under these conditions, approximately 1111 coyotes must be collected in order to show the status of this one food. If d could be increased to 5 per cent, it would be necessary to collect only about 400 coyotes.

AVERAGE QUANTITY EATEN OF ONE FOOD

ANIMALS ACTUALLY EATING THE FOOD—For the time being, only a restricted part of the sample is considered; that is, only animals whose stomachs contain some of one particular food. As a result, the mean volume is found by dividing the total volume eaten by only those stomachs which contain some of it.

Let e be the allowable amount by which the mean volume of the one food eaten by sample animals may deviate from the mean volume eaten by the whole population, and let e be based always on the restricted animals whether in the sample or the population. The sample size required for estimating with 95 per cent confidence the mean volume (or weight) eaten of one food is given by the formula

$$[2] \quad N = \frac{4\sigma^2}{e^2}$$

which is a slightly different arrangement of the formula given by Snedecor (1946: 457).

In order to compute N it is necessary to know σ, which is the standard deviation of the mean volume of the given food eaten by the restricted population. (The value σ must be based on only those animals which actually ate some of the food). Again, an estimate of σ based on past data or experience must be used, or a small series of stomachs can be collected in order to obtain an estimate.

In an earlier study, it was required to estimate the value of N as it applied to sorghum eaten by bobwhite quail (Hanson, 1953: 58-59). Bobwhite were collected,

presumably at random, from the sandsage community of northwestern Oklahoma. All but a few of the birds were taken during one season of one year. Of the 235 stomachs collected, 91 contained sorghum. The standard deviation of the mean volume of sorghum, as based on the 91 birds eating this food, was $\sqrt{4.71}$. Using this value and an allowable error of 0.4 cc., the following estimate was made: $N=\frac{4x4.71}{(0.4)^2}=117.$

Therefore, it was necessary to examine 117 crops which contained at least a trace of sorghum in order to assure 95 per cent confidence that the estimate of the mean volume of sorghum in the 91 sample birds was within 0.4 cc. of the true mean volume in the entire restricted population.

Sometimes it may be desirable to estimate N with a different degree of confidence than is given by Formula [2]. The quantity 4 in the numerator of that formula assures about 95 per cent confidence, providing that the value for σ is quite accurate. If it is desired to estimate N with 99 per cent confidence instead, the appropriate value for t^2 may be substituted in place of the quantity 4 in Formula [2]. The value of t for several sizes of sample and several confidence levels can be found from the table given by Snedecor (1946: 65). When looking up t, it must be remembered that the sample size applies only to those stomachs which contain the particular food.

It should be pointed out that e in this paper will not be exactly accurate even if the true values of p and σ^2 are obtained in each case.

However, e will probably be accurate enough for most purposes. If it is desired that the allowable error e be exactly accurate, then a refined technique must be used. In most cases it is doubtful if the refined method is warranted unless it is extremely urgent that the allowable error is exactly e with no possible small deviation on either side of e.

ANIMALS NOT EATING THE GIVEN FOOD—It must be remembered that the section just discussed dealt only with restricted animals or those whose stomachs contained at least a trace of the given food. Formula [2] cannot be used to estimate the total number of animals needed (both those eating and not eating the given material) but only those actually eating it. If this formula is to work correctly, the measurements of volume must be distributed normally. But stomachs which have none of the given food will cause frequencies to accumulate at the zero measurement. Hence, the distribution of measurements will depart greatly from normality if stomachs which contain none of the particular food are included. This explains why it was necessary in Formula [2] to use only stomachs which had some of the selected food.

In spite of this, it is relatively easy to determine the total number of animals which must be collected. Formula [2] indicates how many animals eating the given food must be taken. Then the stomachs may be opened soon after they are secured, and a cumulative total of the number containing the particular food may be kept. Collecting can be continued until enough stomachs which contain the food are found.

Animals sometimes are collected in one season for later analysis. By then it might be too late for further collections. If it is not possible to examine the stomachs soon after they are collected, the total number required may be estimated by a few additional calculations. Let the total number of stomachs needed (both those containing and those not containing the given food) be called N_t. Then N_t may be found from the formula—

$$[3] \quad N_t=\frac{m+2\sqrt{m(1-p)}}{p}$$

where

$$m=\frac{4\sigma^2}{e^2}$$

Formula [3] permits about 95 per cent confidence in the estimate of the mean volume within e units of the true value; m is derived in the same manner as N in Formula [2]. In the sample and the population itself, the mean volume of a food is based again only on those animals which contain at least a trace of the given material. However, N_t in Formula [3] gives the total number of required stomachs, both those containing and not containing the given material.

The estimate of σ, like the mean, must be based solely on stomachs which have some of the given food in them. One must also have an estimate of p. In Formula [3], p must now be expressed in decimal form.

The values σ and p can be estimated from previous collections if it is believed that they are approximately correct and that ecological conditions have not changed greatly. Or a small sample of animals can be collected, their stomachs analyzed, and the values for σ and p to use in Formula [3] obtained.

Unfortunately, the sample size N_t, as determined from Formula [3], will often be too large to be easily collected. If m is quite small and/or p is quite large, the required sample size may be entirely practical. Almost always, though, it will be necessary to collect a much smaller total number of animals if N is computed as given in [2], the stomachs are opened soon after collection, and collecting is stopped as soon as enough stomachs with the given food are found.

SAMPLE SIZE FOR ALL MAJOR FOODS

PROPORTIONS OF ANIMALS EATING THE FOODS—Previously, methods which could be used to estimate proper sample size for one food only were discussed. However, the wildlife worker usually wants to take a sample large enough so that he has the desired accuracy for all major foods, not just one. Here, a different size of sample is required for each material eaten by a different proportion of animals. But the material which comes nearest to being eaten by 50 per cent of the animals will require the largest sample. Therefore, the major food which has p most nearly approaching 50 per cent can set the minimum sample size for all major foods. A sample large enough for it will be large enough for the others. For example, suppose that one major food was eaten by 10 per cent of the animals and that another was eaten by 70 per cent of the animals; the latter would require the larger sample because its value for p is nearer 50 per cent.

MEAN VOLUMES EATEN—When dealing with mean volumes eaten, in contrast to p, it can be assumed that the food which has the greatest range in volume in different stomachs will require the largest sample. Therefore, a sample large enough for the major food with the greatest range in volume should be large enough for all other major foods. A small number of stomachs can first be collected and analyzed. The analyses will then show which major food has the greatest range. Next, the standard deviation of this major food with the greatest range can be calculated and used for σ Formulas [2] and [3]. The resulting sizes of samples, N and N_t, should be adequate for all major foods.

REDUCING SAMPLE SIZE

The value for N in Formulas [1] and [2] and N_t in Formula [3] may be larger than desired. If this is so, the sample size may be reduced in several ways:

1. Reduce the confidence limits to 90 or 80 per cent. This will require looking up the proper value for t^2 and substituting it for the quantity 4 in the formulas used.
2. Increase d or e as the case may be.
3. When dealing with volume, base sample size on foods with a smaller range; when dealing with p, base sample size on foods with p further removed from 50 per cent.
4. In the case of p, split the broad categories of food considered into smaller categories or do just the opposite, whichever will remove p further from 50 per cent. For example, if rodents are one category of food and it is desired to reduce p, the group is split into several kinds of rodents.
5. Sample the animals from a more nearly uniform environment. For instance, reduce the length of time over which the sample is collected, or reduce the size of area from which the sample is collected.

SUMMARY

Statistical methods are given for finding the sample size required to estimate the food habits of a population under different conditions.

The sample size required for one major food is discussed. However, one food can be used to set sample size for all major foods. When dealing with the proportions of animals eating the different materials, the major food which comes nearest to being eaten by 50 per cent of the animals will require the largest sample. Therefore, a sample large enough for it will be large enough for other major foods.

The major food eaten in the greatest range in volume by different animals can be assumed to require the largest sample size. Therefore, a sample large enough for it should be large enough for other major foods.

Methods of reducing sample size are discussed.

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TRANSPLANTATION OF GAME IN EUROPE AND ASIA

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The harmonious adjustment of transplanted animals to the new environment will depend upon full recognition of the following factors: 1) Climate, elevation, soil type, and habitat in the new area must approximate those in the original range of the species (Becker-Dillinger, 1945 and Lindemann 1937a). 2) In order to avoid hybridization with species already present, closely related animals should not be brought in. If the introduction is being made in order to fill a gap left by the extirpation of a native species, it is wiser to attempt the reintroduction of the original animal. 3) The reproductive potential and spreading tendency of the new introduction must be considered in order to avoid bringing in an animal which will increase so rapidly as to jeopardize native animals by too vigorous competition. 4) The presence of natural predators is of great importance in regulating overpopulation and in improving the quality of the species (Lindemann, 1937b, 1950a, 1952, 1954, Lindemann and Rieck 1953).

Unfortunately, the history of naturalization records many disastrous results. Several unfamiliar examples are given here to serve as a warning to those with similar experiments in mind.

Before the revolution of 1917, the Bialowies forest in eastern Poland was managed for decades entirely without regard to ecology, but only for the sake of the Czar's hunts (Romanow, 1932). The large predators such as bear (*Ursus arctos arctos*), lynx (*Lynx lynx lynx*), and wolf (*Canis lupus*) were extirpated and in a very short time, the ungulates reached overpopulation densities. In addition to the closely guarded wisent herds (*Bison bonasus bonasus*), were such large numbers of red deer (*Cervus elaphus elaphus*) and roe deer (*Capreolus capreolus capreolus*), that natural reproduction of the forest trees became impossible. In spite of artificial feeding of the animals, heavy browsing threatened the very existence of the forest. The fallow deer (*Dama dama*), introduced from the Mediterranean region about 1890, were particularly prone to debarking and browsing. They were unsuited to the Bialowies and degenerated in quality, becoming smaller and developing inferior antlers. On the other hand, they reproduced more rapidly than the native species and showed great mobility and tendency to spread. The resultant unrest in the area contributed to the decimation of the valuable red deer herd. Soon all species of the deer family began to show clear signs of degeneration, having lighter weight, smaller antlers, and increased susceptibility to diseases, outbreaks of which had heretofore been sporadic.

However, during and shortly after the first World War, game populations were greatly decreased. The wisent was entirely extirpated in the Bialowies region. The large predators returned to their native haunts and began to exert natural selection upon the game (Lindemann 1950a, 1937b). As a result, fine specimens of red and roe deer

again appeared. The fallow deer, which was dependent upon artificial management, was unable to compete and soon lost out. In 1928 only 15 head were found where there had been 150 head in 1923. Since 1930, no fallow deer have been found in the Bialowies (Lindemann 1937a).

An example of the way in which hybridization can reduce the value of game animals was provided by the introduction in the days of the Czars, of the central maral deer (*Cervus canadensis sibiricus*) from Asia and wapiti (*Cervus canadensis canadensis*) (Romanow 1932). The results of this unconsidered effort to "freshen up" the blood of the native deer were soon evident in the antler formation, which is of prime importance to European hunters. The antlers of the hybrids had fewer points, poorly developed burr, and less spread between the antler tips. The first two of these characters were inherited as dominant traits, the last character as a recessive trait. As a result of only a few crosses, the desirability of the Bialowies deer was greatly lessened. Not until after 1930 did the Polish game managers succeed in weeding out these undesirable characters by selective hunting.

The attempts to acclimatize various fur-bearers in Soviet Russia have resulted in several successes (Ognew 1951). On the other hand, the introductions of the European hare (*Lepus europaeus europaeus*) into the far East, the Siberian mink (*Lutreola lutreola sibericus*) and the squirrel (*Sciurus vulgaris exalbidus*) into central Russia, the beaver (*Castor fiber*) into about fourteen areas behind the Urals, the north Siberian polar fox (*Alopex lagopus*) on the Kola peninsula, the far eastern raccoon dog (*Nyctereutes procyonoides*) into western Siberia, and the Kamchatka sable (*Martes zibellina kamschadalica*) into western Siberia, resulted in only one welcome improvement. Interbreeding of the Kamchatka sable with the native Siberian sable developed a heavier and more valuable fur in the native animal. The introduction of the raccoon dog into Siberia was a dismal mistake. Although it had been brought in as a fur-bearer, its fur was found to be of no value. It adjusted quickly to its new home, and soon was reproducing so rapidly as to jeopardize the native mustelin fur-bearers, with which it came into direct competition for food. According to one observer in the Caucasus, the raccoon dog changed its food habits from fish and crabs in its native home, to game birds, hares, and poultry. This same species, which is called "Ussurian raccoon" by the Russians, was also introduced into the Kalinin area of central Russia, where it is looked upon as a desirable addition to the fauna. Since 1934, it has increased in such a way that the take in the Kalinin area was 150 per cent above that in the far East in 1946.

Mention must also be made of the muskrat (*Ondatra zibethica*), which although originally confined to fur farms, has spread over entire western Europe and has become a notorious agricultural pest. Another attempted fur-bearer introduction was that of the nutria (*Myopotamus coypus*) into central Russia. Because of unsuitable climate conditions, this effort was a failure and the animals disappeared; however, nutria was successful in Armenia, Georgia, and the steppes of Shirwan.

The reintroduction of species which have been extirpated or have been displaced by agriculture is often unsuccessful if the habitat has been so altered by man as to destroy the ecological niche of the animal. A good example of this is the many attempts between 1741–1938 to reestablish the capercaille (*Tetrao urogallus urogallus*) in Europe (Bobak 1952, Lindemann 1951a, 1950b). The new stock from Scandinavia had lived under entirely different ecological conditions, and was unable to survive in the intensely cultivated areas into which it was transplanted. Similar results were had in Warthegau (formerly western Poland) in 1936–1948, where the range was not suitable. On the other hand, capercaille was successfully reintroduced into Scotland and Bulgaria in 1900, and into Poland, Estonia, Latvia, and Lithuania in 1933–1939 (Lindemann 1950b). Besides capercaille, black grouse (*Lyrurus tetrix tetrix*) (Lindemann 1951b), hazelgrouse (*Tetrastes bonasia bonasia*) (Lindemann 1953) and ptarmigan (*Lagopus lagopus rossicus*) were successfully introduced in Poland (1933–1939).

The acclimatization of new species should never be considered in the absence of exact knowledge of the food habits and behavior (for instance, predator-prey relationships, competition for food, ecological adaptation) of native species already occupying the same habitat. In my opinion, the main aim

of game management is to preserve native species; a native species in its native habitat is always the highest goal of the manager. Only in the case of irrevocable impoverishment of habitat do we adopt the radical remedy of introduction of exotics.

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EVALUATION OF THE PELLET GROUP COUNT AS A DEER CENSUS METHOD [1]

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Reliable estimates of deer numbers are basic to effective deer herd management. Michigan's first large scale "any-deer" season in 1952 led to intensive study of available methods of estimating deer population levels. Results of some experimental investigations concerning the potential value of pellet group counts as a deer census method are presented here.

The method was described by Bennett, English, and McCain (1940) and has been subsequently used by a number of investigators. However, only a limited amount of checking has been done on basic assumptions. Perhaps one of the best possible checks on the method lies in its application to an area containing a known deer population. The purpose of this paper is to report such a test and initial results of studies concerning daily defecation rates and rates of pellet deterioration.

[1] A contribution from Pittman-Robertson Wildlife Research Projects W-63-R and W-70-R.

METHOD

The counts here reported have been based on a number of assumptions:

(1) That the average rate of pellet group (single defecation) deposition is approximately 13 groups per deer per day.

(2) That counts made in the spring (April and May) will include only pellets deposited since leaf-fall (October) or that pellets deposited prior to October will be identifiable as such. Also, conversely, that pellets will persist from October to April.

(3) That all groups are correctly identified as such and that none are missed.

(4) That a 1/50-acre circular plot is an efficient sampling unit.

(5) That valid estimates of sampling error are obtained.

The first two assumptions have been subjected to some degree of experimental verification as described below. The third and fourth assumptions have been investigated through studies on areas of known populations and in field experience. The fifth assumption depends on statistical theory and has not been investigated in detail.

Calculation of deer populations from pellet counts has been accomplished from the following equation:

$$\text{Deer per square mile} = \frac{\text{Average pellet groups per plot} \times 50 \times 640}{\text{Days since leaf-fall} \times 12.7}$$

The factors 50, 640, and 12.7 respectively represent the number of 1/50-acre plots per acre, acres per square mile, and average pellet groups per deer per day.

COUNTS ON AREAS OF KNOWN POPULATIONS—Pellet counts were conducted on two areas of known deer populations in 1953, 1954, and 1955. The areas are: (1) the George Reserve, an area of 1200 acres in southern Michigan (see O'Roke and Hamerstrom, 1948); and (2) the Cusino enclosure, a 647-acre experimental area maintained by the Michigan Department of Conservation at its Cusino Wildlife Experiment Station in the Upper Peninsula. Both areas are enclosed by supposedly deer-proof fences and are censused annually by drive-counts. A drive census on the George Reserve is conducted each winter by wildlife management students from the University of Michigan, and the Cusino enclosure is censused several times each year by state prison camp inmates under close supervision of experiment station personnel.

The Cusino enclosure population figures are believed to be exact because a known number of tagged deer were introduced in 1952; several drives were conducted each spring and fall; winter live-trapping and spring fawn searches insured that nearly all deer were identified (tagged); and all deer were temporarily removed during the late winter of 1953–54.

The George Reserve population data may be less exact than those for Cusino since the original herd was introduced in 1928 with population figures thereafter based on single annual drives only; and the fence has deteriorated to some extent with known recent instances of deer passing in and out of the area by jumping the fence. However, there is little reason to believe the population estimates to be in error by more than a few deer, if at all.

The two areas may represent extremes in Michigan's deer range. The George Reserve is in southern Michigan where winter conditions are usually mild and the Cusino enclosure is in the deep snow belt of northern Michigan. Approximate composition of cover types in the two areas is:

GEORGE RESERVE [2]		CUSINO ENCLOSURE	
Mixed hardwoods (mainly oak-hickory)	26%	Upland hardwood (sugar maple-elm)	46%
Tamarack swamp	11%	Lowland hardwood (red maple-cherry)	22%
Brush	6%	Cedar-alder swamp	9%
Bog and marsh	11%		
Grassland	46%	Grassland	23%

Pellet counts on the two areas resulted in the following estimates (deer per square mile):

CUSINO ENCLOSURE

Year	Pellet count estimates	Approximate 95 per cent confidence limits on estimates	Average known population
1953	40.8	29.4 - 52.2	28.8
1954	25.5	18.0 - 33.0	25.0
1955	22.2	13.4 - 30.9	28.1

GEORGE RESERVE

1953	30.7	23.2 - 38.2	32.7
1954	28.4	20.6 - 36.2	36.1
1955	17.3	12.5 - 22.1	37.2

The confidence limits given above are in terms of deer per square mile. They result, of course, from estimation of sampling error in counting pellet groups and do not include estimates of error from other sources (period of leaf-fall, pellet groups deposited before leaf-fall, pellet groups missed, etc.). A component of variation due to estimation of average pellet groups per deer per day (12.7) has been included in computing the confidence limits. However, this component is small enough to be regarded as negligible in most applications.

Both enclosures were sampled on a systematic basis. In the George Reserve about 240 regularly spaced plots have been used at nearly the same points each year. At Cusino, 147 clusters of 3 plots spaced 40 feet apart

[2] From O'Roke and Hamerstrom, 1948.

were taken in 1953 and 148 clusters of 2 plots (the outer 2 plots of 1953) in 1954 and 1955.

Inspection of frequency distributions of pellet groups per plot shows decidedly skewed distributions. Confidence limits have been computed on the basis of normal theory on the assumption that the importance of exact confidence interval statements is overshadowed by other considerations, *e.g.*, the first three assumptions given above. Cochran (1953, pp. 22–27) indicates that the normal approximation is generally satisfactory even with markedly skewed distributions unless very exact statements of upper and lower limits are needed.

Detailed investigation of statistical aspects of pellet-count sampling seems worthwhile, particularly in regard to the value of various sampling methods. However, for purposes of the present paper, perhaps the essential aspect is one of emphasizing the necessity of considering "chance" or "sampling" errors, as well as possible sources of bias in designing and evaluating results of pellet group surveys.

In the surveys reported above from 200 to 400 1/50-acre plots have given estimates ranging from 2 per cent to 53 per cent in actual error. Differences between estimated and actual populations have been expressed in three ways below:

CUSINO ENCLOSURE

	1953	1954	1955
Error as per cent	+41.7%	+2.0%	−21.1%
Error in deer per square mile	+12.0	+0.5	− 5.9
Probability of observed error as chance occurrence	.035	.897	.413

GEORGE RESERVE

	1953	1954	1955
Error as per cent	−6.1%	−21.3%	−53.4%
Error in deer per square mile	−2.0	− 7.7	−19.8
Probability of observed error as chance occurrence	.596	.051	very small

The line "probability of observed error..." indicates how likely the observed error is on the basis of chance causes alone. Thus, for the 1953 Cusino estimate we might expect as large a difference as this in slightly less than 4 out of 100 such samples. An error as improbable as this might well be assigned to causes other than chance. In this case, it seems possible that the over-estimate was due to the inclusion of pellets deposited before leaf-fall since no effort was made in this particular survey to discriminate "old" pellets in areas where leaf-fall was scanty.

The 1955 George Reserve estimate is definitely biased. A recheck of 13 permanently marked plots four weeks after completion of the survey yielded a count of 25 pellet groups where only 13 had been previously tallied. A few of these pellet groups could conceivably have been deposited after the original count, but only one group was judged fresh enough to be so classified. It seems certain that estimates from this survey were seriously affected by failure of the observers to make an adequate search of the sample plots.

Although the 1955 Cusino estimate does not show statistically significant evidence of bias, personnel conducting the survey believe that, because the survey was phenologically several weeks later than in previous years, some pellet groups may have been missed because of the presence of new vegetation and consequent disturbance of the leaf mat.

Further evidence of errors due to undercounting and/or vegetative disturbance is available from surveys conducted over the northern Lower Peninsula (about 16,000 square miles) in 1954 and 1955. The 1955 estimates were so much lower than those obtained in 1954 that it seems certain the difference cannot be ascribed to either sampling error or changes in deer populations.

DAILY RATES OF PELLET GROUP DEPOSITION—Daily defecation rates were investigated fairly intensively in 1953 and 1954 at the Cusino and Houghton Lake Wildlife Experiment Stations. The largest volume of information was obtained in conjunction with a deer-feeding experiment at Cusino in the winter and spring of 1954. Records were kept on 12 pens of 3 deer each. Pellet groups were counted 24 hours after a snow-fall. A total of six counts was made during February, March, and April of 1954. Half of the deer were fawns and the balance were adults; all but one of the adults were does. Six different diets of natural browse ranging from good nutrition to severe starvation were used. Diets and average pellet groups per deer per day were as follows:

	DIET			
	"Cafeteria"	Swamp conifer	Swamp hardwoods	Hemlock hardwoods
Adults.....	14.6	13.2	13.0	12.8
Fawns.....	13.5	12.3	12.6	10.8

	DIET—(*Continued*)		
	Fire succession	Mixed conifer-upland hardwoods	Average for all diets
Adults.....	12.7	13.2	13.3
Fawns.....	11.8	11.5	12.1

An analysis of variance of the basic data indicated significant differences (at the .01 level of significance) between diets and between ages. Absence of significant interaction between ages and diets suggests that the diets did not affect daily rates of fawns and adults differently. Error mean square from the analysis was 0.98.

The average rate for the entire group of deer was 12.7 pellet groups per deer per day which is exactly the rate previously reported by other workers. (McCain, 1948).

An earlier (1953) study at Cusino using 4 deer for a total of 73 deer-days gave an average rate of 13.0 pellet groups per deer per day and a similar experiment at the Houghton Lake Station resulted in an average of 12.4 pellet groups per deer per day for 9 deer-days. Results of these studies are not significantly different from those obtained in the more detailed investigation other than that there was some evidence that individual deer may show consistently high or low daily rates.

From the available data, it appears that the average pellet group conversion factor (12.7) might be increased or decreased in accordance with the age composition and winter diet of the particular herd being censused. However, under the usual circumstances, we do not have sufficiently accurate information for such adjustment. For practical field use, a rate of 13 pellet groups per deer per day is probably sufficiently close to actuality since adult deer predominate in many herds and nutritional levels may be better than some of those used in the experiments discussed above.

Variability of the daily conversion rate is rather low, the coefficient of variation being about 18 per cent, and 95 per cent confidence limits on the estimated average daily rate (12.7) are 12.4–13.0 from the feeding experiment data.

PELLET "LIFE" AND ERRORS DUE TO LEAF-FALL—Experiments concerning pellet deterioration are at present being conducted at the Cusino and Houghton Lake Experiment Stations. Some general information is presently available but any definite conclusions will require observation of marked pellet groups over several years.

At present it seems that most pellet groups can be roughly classified as to the season of the year when they were dropped. "Winter" pellets are normally elongated and symmetrical and usually brownish in color. "Summer" and "fall" pellets are ordinarily more spherical in shape, usually more or less deformed, and often black in color. "Spring" pellets are loosely formed, due no doubt to a high percentage of succulent material in the spring diet, and decompose rapidly.

Summer and fall pellets deposited under dry conditions may harden and persist for long periods. Some such groups under observation at Cusino have remained unchanged for over three years. When these groups are encountered in areas of scanty leaf-fall they may be counted as being from the current year.

Pellets in swampy areas may persist for as long as two years, but usually change enough to be identified as "old" pellets.

Errors associated with leaf-fall have not been well determined. In Michigan, the period of major leaf-fall in 1953 ranged from October 10 to October 27. Additional difficulties result from a continuous light fall of oak leaves throughout the winter and from wind disturbance of leaves in fall and spring. In some areas there is little or no leaf-fall (grassland in particular) so that an effort must be made to determine whether or not a given group was deposited prior to general leaf-fall.

DISCUSSION

While there are as yet a number of uncertainties in applying the method, the pellet count appears to have potentially an important place in deer censusing. A particular advantage over other methods is that pellet groups provide a persisting record of the presence of deer whereas visual or track counts depend on current activity of deer and may thus be affected by the presence of the observer and weather conditions. Similarly, sampling problems are lessened by the permanence of this record of deer activity.

Difficulties inherent in the method include purely mechanical problems such as determining when pellets were deposited, and the necessity for making allowance for losses of deer during the period covered (from hunting, illegal kill, and "natural" causes) to provide a current population estimate. Results of our most recent (1955) counts have been sufficiently lower than known populations (or reasonable expectation of population levels) to indicate the presence of some serious systematic error(s) in application of the method. Some precautions against such bias are proposed as follows: (1) conducting the surveys as early in the spring as possible, (2) conducting training courses for all personnel involved in the survey, and (3) introduction of a system of rechecking some sample plots by a second observer. Investigation of the efficiency and accuracy of other plot sizes and shapes may also be worthwhile.

Effective use of the method may also be reduced because of a factor entirely unrelated to its mechanical efficiency—the problem of describing the method to the general public. Most probably fecal counts do not sound very scientific to the average sportsman. One way of avoiding the issue lies in the use of the rather grandiose term "Deer Activity Index" to describe results obtained from pellet counts, browse surveys, and sundry other observations. It seems likely that anyone using the method should be prepared for the eventual necessity for explaining the whys and wherefores to a critical audience.

SUMMARY

Pellet counts as a method of estimating winter deer populations have been subjected to three years' study in Michigan.

Application to two areas of known deer populations provides a partial check on accuracy of the method. Results to date indicate that the method may be subject to serious errors from either natural causes or observer error or both. However, it seems reasonable to believe that such errors may be controlled sufficiently to permit use of the method as a reliable means of censusing.

Rates of pellet deposition, although differing between adult and juvenile deer and varying with diet, are sufficiently uniform so that an average rate of 12.7 (or, for convenience, 13) pellet groups per deer per day can be used with assurance of very little error from this source.

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FURTHER ANALYSIS OF METHODS FOR CENSUSING WINTER-LOST DEER

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Results of a study testing five methods for censusing dead deer were presented by Robinette *et al.* (1954). The tests were made on restricted units of Utah winter deer range on which there were known numbers of dead deer or randomly placed burlap sacks simulating dead deer. It was concluded that Hayne's (1949) modification of King's grouse census method and Webb's (1942) snowshoe hare census method were not adapted to censusing inanimate objects. King's grouse census method, the Lincoln Index (Lincoln, 1930), and Kelker's (1945) belt transect method gave acceptable results when certain precautions were taken to eliminate bias.

Hayne, in a letter of March 29, 1954 to the senior author, suggests that some constant bias might have been present in our surveys to explain why King's method should give acceptable results whereas his did not. He believes that there may have been some tendency for the observer to search more intently at the sides than straight ahead, a tendency which would have the effect of inflating population estimates from both methods because of shortened sight distances. Hayne further suggests studying the distribution of sacks or dead deer from the line of travel for various sight distance classes as a means of detecting this possible source of bias. This suggestion was tried but no definite conclusions were reached because of problems in analysis.

However, it appears that a bias prevailed throughout our census surveys as revealed by a study of sighting angles, i.e. the angles from our line of travel at which the dead deer and sacks were first observed. Recognition of this added source of bias has prompted the writers to modify conclusions regarding use of King's method on dead deer surveys. Hayne (*op. cit.*) has pointed out that theoretically the mean flushing or sighting angle should be 32° 45′ 15″. The mean sighting angle for 597 observations on our Cedar Fort sack surveys was 48° 34′; for 302 observations on the Oak Creek sack surveys it was 48° 42′; for 117 dead deer observed afoot in the juniper-sagebrush type it was 41° 44′; and for 227 dead deer observed from horseback in the same vegetative type it was 42° 38′. All four angles exceed significantly the theoretical angle at the 1% level. This condition indicates that there was a delay in our average observation or, in other words we were not seeing the objects at the instant they first came within visible range.

Sighting angles in excess of the theoretical in turn mean that our sighting distances were less than they should have been. This error would result in inflated population estimates by both Hayne's and King's methods. The writers believe that the delayed observations and consequent excess angles have resulted through inability of the observers to simultaneously cover a 180-degree observational arc as they moved along census lines. For example as an individual looks for carcasses or sacks on one side of his census line and continues to move forward he might be well within

visual range of sacks or dead deer on the other side before turning his head to actually see them.

The importance of delayed observations upon census results can be appreciated through further examination of the first Cedar Fort sack survey data. The mean sighting distance for 153 observations was 45.5 feet and the mean perpendicular distance from the census line was 34.9 feet. These mean values imply a sighting angle of about 50° 5′ (actually it was 53° 41′ as derived by averaging all of the 153 angles). A mean perpendicular distance of 34.9 feet and a sighting angle of 32° 42′ 15″ yields a mean theoretical sighting distance of 64.6 feet, an increase of 42 per cent over the actual mean sighting distance of 45.5 feet. Population values for both King's and Hayne's methods are both decreased by nearly 30 per cent when the theoretical sighting distances (obtained by multiplying each of the actual sighting distances by 142 per cent) are used.

Similar computations for the three remaining Cedar Fort surveys revealed mean theoretical sight distances exceeding the actual percentages by 16, 26 and 18. The overall effect of the longer theoretical sight distances was to decrease the population estimates for the four surveys by about 21 per cent for both King's and Hayne's methods. Population results were decreased about 22 per cent for the four Oak Creek sack surveys when the theoretical sight distances were used. Revised population values on the basis of the theoretical sight distances for Hayne's and King's methods are given in Table 1.

Use of the theoretical sight distances reduces mean results from Hayne's method from 330 to 257 on the Oak Creek area and 313 to 246 on the Cedar Fort area. Results from King's method were reduced from 190 to 151.

Confidence limits at the 5% level listed in Table 1 for Hayne's method embrace the known population of 200, but barely so. If the eight values for Hayne's method are combined, confidence limits at the 5% level are narrowed to 219-284 with a probability less than 0.01 for the "t" value. Thus even with adjusted sight distances Hayne's method still fails to give results that are fully acceptable. Values from King's method on the Cedar Fort area are likewise unacceptable when adjusted sight distances are used.

TABLE 1.—POPULATION ESTIMATES OF BURLAP SACKS ON TWO AREAS BY HAYNE'S AND KING'S CENSUS METHODS IN WHICH THEORETICAL SIGHT DISTANCES WERE USED. KNOWN POPULATION—200

	Area—Oak Creek[1]		Cedar Fort
Survey No.	Method—Hayne	Hayne	King
1	318	292	156
2	238	252	150
3	264	210	152
4	207	231	147
Mean	257	246	151
Departure from 200	+28%	+23%	−24%
Confidence limits (5% level)	182–332	191–302	145–157
Probability of "t" value	.09	.08	<.01

[1] Results from King's method not computed for Oak Creek area because of another type of bias in field data (Robinette *et al.* 1954).

In addition to the foregoing procedure of sight distance adjustment (i.e. where each value was increased by the same percentage) the writers calculated a sight distance for each sack observation by dividing the observed perpendicular distance by the sine of 32° 42′ 15″ (the mean theoretical observational angle). Sight distances computed in this manner gave essentially the same results for King's method but considerably more for Hayne's than when every sight distance was increased by the same percentage. The increase in population estimates from Hayne's method appears accountable to the very short calculated sight distances (many of which were even shorter than the actual sight distances) resulting from short perpendicular distances—especially those less than 10 feet. A study of Hayne's formula will show that short sight distances carry many times more weight in population determinations than do the longer ones.

Even though a bias prevailed throughout our surveys, as revealed by sighting angles greater than the theoretical, this source of error appears to explain but part of the disparity between results from Hayne's method and the known population. At present we can see no way in which Hayne's

method can be acceptably used on dead deer surveys or surveys for other inanimate objects either through modification of field procedures or correction of sighting distances.

It is perhaps possible to obtain observational angles in the field which more nearly conform to the theoretical than what we obtained on our surveys, by having the observer move more slowly along the census lines thereby permitting more frequent side observations. This practice should enable the observer to see objects to be censused more nearly at the instant they come within sight. However, it seems doubtful that census results obtained in this manner would differ greatly from those in which the sighting distances are corrected to a theoretical observational angle as outlined above.

It appears from the reanalysis of our data that King's method has by chance given us satisfactory results under the particular conditions with which we worked. Results can conceivably be influenced by many factors including observers, vegetative cover, etc. However, it may be of interest that there were no significant differences between the sighting angles obtained by the six participants on the Oak Creek sack surveys. An analysis of variance gave an F value of 1.03 attributable to this source of variation which is considerably less than the 5% point of 3.09. It should be recognized, however, that lack of significance in the sighting angles obtained by the individuals may have been attributable to prior training together—resulting in members of the survey crew traveling at about the same rate of speed, etc.

Even if the role of different individuals upon census results from King's and Hayne's method can be discounted it is doubtful that the influence of various vegetative cover types can be. It seems probable that King's method might give a substantial underrun in an area supporting little vegetal cover because such conditions would permit more rapid visual coverage and probably smaller sighting angles than we obtained in the juniper-sagebrush type. On the other hand the influence of vegetal cover may be offset in part by the participants moving more slowly in dense cover than in sparse cover. The fact that the mean sighting angle for 899 sacks was between 48 and 49 degrees as opposed to one of about 42 degrees for 344 dead deer raises further doubts regarding uniformity of results to be expected from King's method. There is here some indication that the object being censused may influence the sighting angles and consequently census results for methods using sight distances. Inconclusive evidence has likewise indicated that direction of the census line may influence results, possibly because of the influence, in turn, of sunlight and shadows upon visibility conditions. Our data suggest that if the mean sighting angle on a survey is somewhere between 45 and 50 degrees reasonable accuracy in census results from King's method might be expected.

In light of the foregoing reanalysis we should like to amend our original recommendations of methods to be used. We now believe that Kelker's method, covering a strip of predetermined width, and the Lincoln Index are best in the order named for practical field use. We do not wish, however, to eliminate King's method from consideration. It was of interest and possibly of significance that population results by King's method using adjusted sight distances (Table 1) attained greater uniformity than when actual sight distances were used. Should added study show similar uniformity with values averaging about 25 per cent less than the true population there may be merit in using King's method with adjusted sight distances on dead deer surveys. Results might then be increased by one-third.

The first two of the three methods recommended above require the user to plan his course farther in advance of his travel than the distance at which dead deer or other objects being censused can be observed. This precaution is essential in preventing bias in measurement of the perpendicular distance of a dead deer from the line of travel (Kelker's method) and in the determination of whether the carcass lies within the census strip (covering a strip of predetermined width). Straight census lines along compass bearings are perhaps best but deviations can be made to circumvent impassable ledges, washes, marshes, etc., if the aforementioned precaution is observed. We believe it a fruitful procedure to record all perpendicular distances even if the method of covering a strip of predetermined width is being employed. An-

alysis of the resulting distances assists the censuser in determining the optimum width of strip which can be covered under prevailing conditions of cover and topography.

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DETERMINING STRUCTURE IN COLUMBIAN BLACK-TAILED DEER POPULATIONS [1]

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In order that the big-game biologist may plan or assess management practices he must often determine the sex and age structure of a deer population. This is attempted through analysis of such population characteristics as sex ratios, old-young ratios, and population density. Adequate field techniques for determining these population qualities are still being developed.

In the course of detailed studies of the Columbian black-tailed deer, *Odocoileus hemionus columbianus* (Richardson), the authors have compared various methods of determining sex and age structure in several populations. Such methods are commonly known as classification counts (Leopold *et al.*, 1951) or herd composition counts (Longhurst *et al.*, 1952). In taking such counts two problems must be met: 1), how to separate accurately the age and sex classes, and 2), how to obtain a representative sample of the population.

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The studies were carried out in brush-covered hills lying about five miles southwest of Lakeport, California. The terrain of the study region is much dissected, with steep slopes and heterogeneous vegetation. The elevation of the study zone extends from about 1500 to 2700 feet above sea level. It is to this region and zone, and the deer inhabiting it, that the rest of this paper applies, except where specifically noted.

The deer are non-migratory and spend the year on relatively small home ranges (Dasmann, 1953). The topography lends itself well to observation of deer; almost every slope may be observed from an opposite ridge, and even dense brush appears less impenetrable when the observer looks at it across a canyon with the sun at his back. These factors have made it possible for us to follow intensively the structure and density of the deer population on a 400-acre area, and on a less intensive basis adjoining populations occupying about ten square miles. Knowing these populations on a continuing basis, recording changes from month to month, we have been able to test and compare various methods of determining population

structure and density. The results form the basis of this report.

FIVE-CATEGORY HERD COMPOSITION COUNTS

It is a common practice for deer workers to make three-category herd composition counts in which a determination is made of relative numbers of bucks, does, and fawns (Leopold *et al.*, 1951). Such counts are often taken as the basis for estimations of reproductive success. However, the "doe" category contains both adult does and yearling does. Yearling does are ordinarily non-producers; that is, does usually breed for the first time as yearlings (at about 17 or 18 months of age) and produce their first fawn when they are themselves two years old. There are many exceptions to this among white-tailed deer (*O. virginianus*) on good range (Cheatum and Severinghaus, 1950), but among mule deer (*O. hemionus*) production of fawns by yearlings is rare (Rampont, 1926, Shantz, 1943, Robinette and Gashwiler, 1950, Crane and Jones, 1953). When there is a single "doe" category, last year's doe fawns are lumped with producing does. If fawn survival to yearling age has been high, the "doe" group seems proportionately large compared to the crop of new fawns, hence it seems that production has been low. If fawn survival to yearling age has been low, production of new fawns may appear high.

The following example will serve to illustrate the possible error that may result from a failure to separate adult does from yearling does:

Year	Adult Does	Yearling Does	Fawns	Ratio Fawns : : 100 adult does	Ratio Fawns : : 100 does
1.....	100	50	100	100	67
2.....	100	20	90	90	75

In Year 1 the fawn production and survival were higher than in Year 2. This is apparent when yearlings are classified and the ratio between fawns and adult does is obtained. If, however, yearlings are not classified it appears from the doe: fawn ratio that the Year 1 was more favorable than Year 2.

To avoid such errors it is necessary to distinguish the yearling class as a separate entity, divided into yearling bucks and yearling does. If this is done, a five-category herd composition count is the result; the categories being: adult bucks, yearling bucks, adult does, yearling does, and fawns. With such a count several types of information are provided: 1) current year's natality; 2) previous year's fawn survival; and 3) sex differences in fawn mortality.

Some workers have attempted to avoid the difficulty of separating adult and yearling does in their classifications by determining the number of yearling bucks in the population, using antler characteristics as a criterion, and assuming that the number of yearling does is equal to the number of yearling bucks. It has been shown in an earlier publication (Taber and Dasmann, 1954) that this is an unjustifiable assumption. Sex differences in mortality rate among fawns may result in a yearling sex ratio which departs markedly from the assumed 50: : 50. In one of the study populations the yearling sex ratio has varied over a three-year period, ranging from 80♂♂: : 100♀♀ to 29♂♂: : 100♀♀.

CRITERIA FOR SEPARATING AGE AND SEX CLASSES

The principal objection to using five-category counts is that yearlings cannot be distinguished from adults with adequate accuracy. Nevertheless, we have found various characteristics within each age-class in our deer which serve to separate the classes successfully. Use of these characters is facilitated when deer are in family groups. These groups may consist of a doe and her fawns only, or it may include yearlings, or even two-year-olds. Members of such a group are readily compared with one another. Distinguishing criteria are size, conformation, coloration, and behavior. The way in which these vary between sex and age classes is summarized in Table 1.

No method applicable in the field will yield complete accuracy. A certain amount of error is introduced by anomalous individuals, such as horned does or fawns born out of season. Additional error is introduced by mis-classification of normal deer. Exercise of careful study at proper seasons will keep this error to a practical minimum.

EFFECTS OF SEASON ON COUNTS

Since comparison is often a necessary basis for distinguishing age and sex classes,

TABLE 1.—CRITERIA FOR DISTINGUISHING SEX AND AGE CLASSES OF COLUMBIAN BLACK-TAILED DEER

Character	Adult Bucks	Yearling Bucks	Yearling Does	Adult Does	Fawns
Antlers	Present March-December; pedicels visible January-March. Often 2 or more points on each. If unbranched, curved postero-laterally and relatively heavy in beam.	Unbranched, straight and under 7″ long. Relatively narrow in beam.	None	None	Antler bumps visible in males about December.
Body size and shape	Large and massive	Slender and long-legged. Noticeably smaller than adults in July. Less so in December.			Noticeably smaller than other classes
Body pelage: color	Tend to begin fall molt before other classes	Follow adult bucks in entering fall molt. Pelage often glossy.		Tend to fall molt later than other class, especially if nursing	Spotted coat until about September
Head shape	Deep-headed with relatively short ears.	Fawn-like in July. Less so in December.		Long-muzzled, flat-headed, often wrinkle faced	High-crowned, short-headed, blunt muzzled. Long ears in proportion to head size.
Face markings	Black or dark inter-orbital mask and contrasting white or gray muzzle. Contrast increases with age.		Inter-orbital area brown or grey. Muzzle grows lighter with age. Less facial contrast than adult ♂♂		Male fawns often have faint beginnings of black mask and light muzzle.
Neck	Thick, esp. in October-November	Thick, but not as thick as adult bucks	Intermediate between fawn and adult doe	Long, thin, often ewe-necked, esp. when old	Relatively short and thick
Ear position	Tend to hold ears in position approaching horizontal.		Tend to hold ears in position approaching vertical.		
Behavior	Separate from family group, often with another buck	Sometimes in family group but often separate from it. Often with other bucks. Sometimes playful.	Usually in family group. Brings up rear when family moves away from possible danger. Often antagonistic toward fawn. Gives way to adult doe. Sometimes playful.	Dominant in family group. Often antagonistic toward yearling. Takes lead in traveling. Seldom plays.	Tends to follow doe closely. Often playful.

counts are most accurate at seasons when deer are found in family groups and no single class is unusually conspicuous or retiring. There are only two seasons in our area when such conditions prevail. One period extends from mid-July, when fawns are about two months old and consistently follow the does while feeding, to early August, when older bucks no longer appear in the open during daylight. The other period begins early in December, after effects of the rut have worn off, and ends when yearling bucks begin to shed their antlers, late in December. Table 2 summarizes the way in which seasonal activities influence visibility of the various classes of deer in Lake County.

In other areas optimum periods for making herd composition counts will probably be different. Thus in the central Sierra Nevada where peak of fawning may occur in mid-July, the middle of September would perhaps correspond most closely to the beginning of the first period in Lake County. In the San Francisco Bay area the middle of June would correspond. The equivalent of the second period in Lake County would

TABLE 2.—THE VISIBILITY OF EACH OF FIVE CLASSES OF DEER ACCORDING TO THE SEASON

	Activity	Adult Bucks	Yearling bucks	Adult does	Yearling does	Fawns
May	Fawn-drop			Less conspicuous because in heavy cover		
June				Family groups re-assemble		Fawns more apt to accompany does in evening than in morning
July	Mid-month: fawns following mothers		May be only loosely attached to family group	Family groups well established		
Aug.	Hunting season August 10th. Hot weather.	Early August older bucks retire to heavy cover	Family groups frequently separated by hunting season commotion			
Sept.	Hunting season closes mid-September. Hot weather.	Older bucks remain in heavy cover		Family groups re-established		
Oct.	Cooler weather. Beginning of rut.	Bucks emerge from heavy cover and actively roam		Family groups disorganized by rut		
Nov.	Breeding first two weeks of month	Peak of buck activity conspicuous at all times of day		Does in heat, leave family groups.	Spend more time than usual in heavy cover	
Dec.	End of rutting activity. Antler shedding by adults, then young bucks, late in month.	Bucks no more active than other deer.		Family groups re-established		Buck fawns often partially independent of family groups
Jan.	Deer in open areas on ridges and south-facing slopes					
Feb.	Deer in open areas, ridges and south-facing slopes					
March	New antlers become noticeable late in month on prime bucks.			Does begin to act antagonistic toward family members.	Begin to withdraw from family groups.	Begin to separate from doe.
April	Does drive their families away as fawn-drop approaches.			Antagonism grows active.		Begin to withdraw from family group.

perhaps fall in January in the central Sierra Nevada.

It has been a common belief among deer workers in the western United States that the best time to make herd composition counts is during the rut (Leopold *et al.*, 1951). During the rut, however, bucks are unusually active and conspicuous and family groups tend to be disorganized. The net result is that counts taken at this time tend to err in favor of mature bucks and to be low in fawns.

EFFECTS OF WEATHER AND TIME OF DAY ON COUNTS

During those periods when conditions are seasonally favorable for obtaining a representative sample of the population, the classification may be further affected by weather and time of day. We have obtained best results during early morning feeding periods on days when the weather was clear and calm. If the observer arrives at an observation point before sunrise on such a day, the deer can be watched as they come out to feed. Duration of this feeding period varies. In summer deer tend to bed one or two hours after sunrise; in winter they often feed irregularly all day.

Deer may be out feeding on overcast or rainy days, but at such times visibility is restricted. Early morning sunlight on clear days gives excellent visibility not only because the air is relatively free of dust and heat-waves, but also because light from the sun is reflected from the deer's coat directly back toward the observer, causing the animal to stand out conspicuously.

Strong winds may cause deer to seek sheltered spots. Unless all such locations are visible from the observation point calm days are preferable for observation.

TECHNIQUES OF OBSERVATION

Accurate classification requires the scrutiny of each individual. Maximum range at which classifications are made, on any given day, should not exceed the distance at which antlers of a yearling buck can be distinguished. Undisturbed deer, which may be observed for long enough to re-check first judgments, may be classified more accurately than disturbed deer, which may not remain in sight long enough for a re-examination.

The most accurate herd composition counts have been found by us to be those made by an observer in a fixed position from which up to 200 acres of brushy hillside could be surveyed. If the sun is kept at the observer's back, one exposure may be watched in the morning and another in the evening. The best available optical equipment should be used; binoculars ranging from 8x40 to 10x50 are useful in searching the area and a telescope of from 20x to 40x permits close examination of individual deer.

Herd composition counts are best taken by men who are familiar with the habits and characteristics of deer and who have spent considerable time in the field actively observing deer prior to the period of counting.

USE OF COUNTS AS CENSUSES

The foregoing has been concerned with the determination of population structure, which is the usual reason for making herd composition counts. However, under the circumstances of our study, counts can also be used to indicate population density.

During the seasons propitious for accurate counting, deer of all classes show a similar response to sunshine on cool mornings. When the sun rises, practically every deer will stand in the rays for warmth, thus being revealed to the observer whose line of sight parallels the sun's rays. The position of each deer is plotted on a topographic map so that individuals may be distinguished and movements noted. Constant observation over a period of two hours following sunrise will reveal practically every deer within the restricted field of view. A number of such observations are made on subsequent mornings, a record being kept in each case of the number of acres under observation, including contiguous shady slopes not actually searched. When each count is weighted according to number of acres covered, and all counts totaled, a measure of population density is obtained.

SUMMARY

A method of herd composition counting is described in which five categories are used: adult bucks; yearling bucks; adult does; yearling does; and fawns. Criteria for distinguishing these five classes are presented.

The best seasons for counting are found to be late July and December, when the deer are in family groups, which facilitates comparison, and no age or sex class is more or less active than any other.

The best observation periods are morning and evening feeding periods of clear, calm days.

The favored observational method is that of searching a limited area, looking away from the sun, from a fixed vantage point. This yields an accurate count and may also be used to determine absolute population density.

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EXPERIMENTS IN LOCATING WILD CHUKAR PARTRIDGES BY USE OF RECORDED CALLS

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The difficulty of ascertaining dispersion of chukar partridges, *Alectoris graeca*, after release has been noted in several states in which chukar projects are in progress. A good census method has yet to be developed.

Since 1951, the New Mexico Department of Game and Fish has released chukars shipped from Turkey by Dr. Gardiner Bump under the Federal Aid in Wildlife Restoration Project W-58-R-3. Chukars have been released in two areas: the Heart Bar Wildlife Area, Catron County, and at Conchas Dam, San Miguel County. In 1954, a three-year life history study was begun to determine dispersion of released birds and those hatched in the wild.

Few birds have been located from releases made in 1951, 1952, and 1953. Those that were reported were as much as 15 miles or more from the release sites. Dispersion in 1954 of 496 released birds has been such that only approximately 30 adults have been found within a four-mile radius at the Heart Bar Wildlife Area and approximately 15 adults near the Conchas Dam release site.

In searching for a method to locate the remainder of the birds, which might move as much as 50 to 100 miles in one year, the first step was to use ten game farm chuckars as callers. These birds were carried in three small portable pens to the release area where they were placed out of sight of each other so that they might call to one another. This calling was then expected to stimulate answering calls from birds in the wild. From this the observer could ascertain the distances birds had traveled from release sites and possibly numbers of birds present.

Disadvantages of using live callers were soon apparent. Travel over rough roads seemed to dampen their desire to call. The birds did not always call when the observer was ready, and when calling did occur it could not be stopped in order to hear answers from wild birds, except by covering the birds' pen with a blanket.

A more practical method to locate the wild birds was by use of recorded chukar calls. A tape recorder was taken to the Carlsbad Game Farm where chukars were being held and recordings were made of their calls, primarily the "community" or "chuck"

call. Upon playing back the calls to the penned birds a vociferous reply was prompt, primarily the "community" call.

It was found advantageous to transcribe these calls on a phonograph record, which was played on a phonograph in a truck equipped with a 6 volt-110 volt AC inverter.

The phonograph caller was first tested on July 20 to 24, 1954 in Colorado. Wayne Sandfort, Wildlife Technician, Colorado Game and Fish Department, was helpful in pointing out areas where chuckars have been known to be present. Chukars answered the caller in 50 to 60 per cent of the tests. Areas in which no answers were obtained either contained adults with broods, or apparently lacked chukars. Broods observed close to the truck did not answer even when calls were played several times.

In one area five males were observed, three of which answered the calls from a hill side about 75 yards above the truck. Two birds moved down the hill toward the truck, calling loudly, while the observers were in plain sight. In another area of thousands of acres of rough canyons and rather heavy vegetation, the call was played in two short intervals of less than 45 seconds. Two chukars immediately answered from the wild. How many other chukars were present was not ascertained at this time. The gratification of hearing birds answer from an area of great vastness was the highlight of this preliminary experiment in Colorado.

A combination of the phonograph caller and a pair of penned game farm callers was used in late July in New Mexico. This offered a chance for the observer to stimulate the penned birds from a distance with the mechanical caller. This situation might best be employed in trapping operations in which penned birds under a trap net might be induced to call until they led wild birds into the area.

Use of good live callers to attract wild birds to the trap or water holes for shooting is reported to have been observed in Turkey by Dr. Bump. The mechanical caller may well take their place. In trapping situations, it may be used as a stimulant to induce live chukar decoys to call.

Areas are limited that can be checked with a truck. Therefore, a small compact phonograph has been used on horseback or on foot in the more inaccessible areas. It is a portable hand-cranked phonograph utilizing a crystal pick-up whereby recorded calls are transmitted through a battery-operated loudspeaker. The phonograph and speaker weigh approximately 12½ pounds. Size of the package is 12″ x 14″ x 8″.

On August 13, the chukar phonograph calls were tried at Pepper Springs near the town of Mina, Nevada. A group of approximately 20 birds, including several young, was observed at the springs. These birds moved up the hill side as the truck approached. After the "community" call had been played perhaps six to seven times one young bird began answering in strong voice. The record was changed to the feeding call and the chukars soon began feeding back down to the springs, perhaps 60 yards from the truck. The warning call was then played; the birds immediately froze and were very alert. They moved back into the bushes, but at the resumption of the feeding call they again moved into the open. Adult birds were more wary than the young and stayed at the edge of the cover.

As the feeding call appears to put the wild chukars at ease, so does the alarm call make them immediately alert. While the feeding call may be best for live trapping operations, the advantage of stopping running chukars by use of the warning call or some other common call is apparent for identification of color marks.

As the result of these preliminary tests with the phonograph caller in Colorado, Nevada, and New Mexico habitat, the following conclusions may be drawn:

The recorded chukar calls were sharp and piercing and may be expected to be transmitted up to one-half mile or more under calm weather conditions.

Usually after the second short transmitted call the wild birds answered. More calls, however, may be necessary to induce an answer.

Broods apparently are not as likely to answer the caller as adults separate from their young, and it may be necessary to play the calls longer in order to stimulate young birds. Whenever adult birds with broods were encountered in Colorado, no answers to the "community" call were given. However, after six to seven calls in

Nevada, a 10- to 12-week-old-bird did answer.

Calls would probably be most profitable when used in early morning and late afternoon when the birds are moving about. Calls in this preliminary experimentation were tried mainly during the middle daylight hours until dusk.

It is believed that use of the caller in fall and winter months when the birds are gathered in coveys would result in greater response to the "community" call.

A portable phonograph, to be used on horseback or on foot, would be a necessity in the more inaccessible areas.

It is believed the phonograph caller will offer a means of checking dispersion as well as a method of censusing chukar partridges.

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INCIDENCE OF SHOPE'S RABBIT FIBROMA IN COTTONTAILS AT THE PATUXENT RESEARCH REFUGE

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Reports of natural occurrence of virus-induced skin fibromas in rabbits have been based, in past years, largely on presence of characteristic lesions on infected animals. An epizootic of fibromas in cottontail rabbits (*Sylvilagus floridanus*) at the Patuxent Research Refuge during 1951 provided an opportunity for further studies of this infection in a wild host. In addition to obtaining information on the prevalence of gross lesions on the rabbits at the Refuge, we also employed another technique for recognizing the presence of the virus. This method involved detection of fibroma virus by a neutralization test for antibodies in the sera.

Virus-induced skin fibromas were first reported by Shope (1932) from a cottontail rabbit shot in November, 1931 in the environs of Princeton, N. J. Subsequently this type of skin tumor has been reported a number of times on cottontail rabbits in the United States, chiefly east of the Mississippi River (Hickie, 1940; Haugen, 1942).

In cottontails, the fibroma virus acts directly on epidermal and connective tissue cells causing the formation of a localized tumor. Shope was able to transmit the fibroma virus to domestic rabbits (*Oryctolagus cuniculus*) by testicular and subcutaneous inoculations. Kilham, *et al* (1953) observed tumors on gray squirrels (*Sciurus carolinensis*) in Maryland which pathologically and immunologically were closely related to the Shope rabbit fibroma. These authors also reported transmission of the gray squirrel strain to woodchucks (*Marmota monax*) and to domestic rabbits by subcutaneous inoculation.

Kilham and Woke (1953) transmitted the fibroma virus from cottontails to cottontails through the bites of fleas (*Cediopsylla simplex*, *Odontopsyllus multispinosus*, and *Hoplopsyllus affinis*) and mosquitoes (*Aedes aegypti*). Kilham and Dalmat (1955) have further shown that besides *Aedes aegypti*, three species of mosquitoes native to eastern United States, *Anopheles quadrimaculatus*,

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Aedes triseriatus, and *Culex pipiens* transmit the causative organism of fibroma. Transmission was accomplished by interrupting the blood meal of mosquitoes feeding on tumors and then allowing them to feed freely on susceptible cottontails. The fibromas which subsequently developed on the legs and feet of the experimental rabbits closely resembled those acquired under natural conditions. Transmission to susceptibles occurred even five weeks after mosquitoes had fed on tumor tissue, suggesting that these mosquitoes may be biological as well as mechanical vectors.

MATERIALS AND METHODS

To determine incidence of fibromas in a native population of rabbits, all cottontails trapped at the Patuxent Research Refuge were examined for visible evidence of tumors. To obtain more complete knowledge of prevalence, sera for neutralization tests were collected from heart or peripheral blood of a series of the rabbits.

Either of two techniques was employed to bleed the rabbits. In one, the animal was immobilized by placing it on its back and tying each limb in a stretched position. For additional security an assistant held the rabbit's head and forefeet in one hand and hind feet in the other with the back of the animal slightly arched. The heart is easily palpated in this position and the posterior end of the sternum serves as a guide to its location. The skin in this area was saturated with 70 per cent alcohol and a 3-inch, 20-gauge needle on a 10 cc. syringe was introduced just below the posterior end of the sternum and moved forward to the target. Five to ten cc. of blood were readily obtained. Care was taken to keep the animal immobile during the procedure to prevent internal bleeding and serious injury to the heart.

The alternative method, more adaptable to field conditions, consisted of removal of blood from an ear vein. Xylol was applied to the ear, causing dilation of blood vessels, and then a vein was slit with a scalpel and the blood allowed to drip into a collecting tube. Alcohol was used to remove traces of xylol after the operation and bleeding was stopped by local pressure.

Sera samples for neutralization tests were stored in a frozen state and, prior to use, were inactivated at 56° C. and diluted 1:2. The OA strain of the fibroma virus (Shope, 1932) was employed, diluted in meat infusion broth so as to contain 10 infectious doses, and was added to an equal volume of serum dilution. All rabbits, prior to inoculations, had fur removed from sides and back with clippers. In these tests, 0.5 ml. of serum-virus mixture was inoculated into the shaved area of the skin. Results were read in 5 days by noting presence or absence of fibromas. The details of these tests have been described elsewhere (Kilham and Fisher, 1954).

OCCURRENCE OF VISIBLE LESIONS

Although 223 cottontails were examined intermittently from March, 1947 to December, 1950, with 77 taken in November, tumors were first observed on 3 of 16 cottontail rabbits shot at the Patuxent Research Refuge in December, 1950. During spring and fall months of 1951, tumors were observed on 12 of 70 (17%) examined (Table 1). None of the 37 rabbits examined in 1952 had discernible tumors and 29 rabbits captured in 1953 were also negative.

One infected cottontail trapped in mid-March, 1951 was maintained in captivity. At capture this animal had a single tumor about the size of a pea on its right hind foot.

TABLE 1.—INCIDENCE OF FIBROMA VIRUS INFECTIONS IN COTTONTAILS AT THE PATUXENT RESEARCH REFUGE AS DETERMINED BY SERUM NEUTRALIZATION TESTS AND PRESENCE OF TUMORS

	Occurrence of Fibromas				Occurrence of Neutralizing Antibodies	
	1947–1950		1951		1951	
	No. Exam.	No. Pos.	No. Exam.	No. Pos.	No. Tested	No. Pos.
January	2	–	1	–	–	–
February	3	–	1	–	–	–
March	11	–	7	3	–	–
April	13	–	1	1	–	–
May	15	–	1	–	–	–
June	13	–	4	–	–	–
July	14	–	11	–	2	–
August	7	–	8	–	6	3
September	14	–	2	–	2	2
October	35	–	13	5	11	5
November	77	–	17	3	13	5
December	19	3*	4	–	2	1
TOTALS	223	3*	70	12	36	16

* All in December, 1950, when 16 cottontails were examined for fibroma.

By mid-May this had entirely regressed leaving no visible evidence of infection. A male cottontail with a fibroma on the right forefoot was trapped at the Refuge on March 2, 1951 and retrapped March 4, 7, and 27. This tumor was reduced in size at each succeeding examination and when last seen was evident only by careful observation. Several cottontails with naturally acquired fibromas have been kept in captivity and although the tumors have increased or decreased in size they have remained evident for periods up to 14 months.

NEUTRALIZATION STUDIES

Cottontails caught prior to July, 1951 were not bled for serum antibody studies. However, beginning in the fall of 1951, blood samples were collected at the Refuge and elsewhere, and the sera checked against Shope (OA) fibroma virus as described above. Results obtained with neutralization tests appeared to be highly specific. The only positive tests were from cottontails either bearing fibromas or coming from the enzootic area at the Refuge. Many of these positive sera neutralized 100 to 1000 infectious doses of fibroma virus. Cottontails obtained away from the enzootic area had neither fibromas nor circulating antibodies. The control group included 70 cottontails caught in January and February, 1953 in Rockville, Maryland[3] and over 30 cottontails obtained from dealers in Kansas and Arkansas.

Three cottontails from the Refuge had fibromas but no detectable neutralizing antibodies. These cases presumably represented young fibromas, as antibodies may not appear in the serum until 2 or more weeks after fibroma development has begun (Kilham and Fisher, 1954). Five rabbits had both fibromas and serum neutralizing antibodies. Eleven animals showing no evidence of tumors gave positive tests when sera were checked against the Shope fibroma virus. Presence of serum antibodies in animals without fibromas is probably indicative of previous infection with fibroma virus.

For the 13 months December, 1950 to December, 1951, the period of the epizootic according to our data, 86 cottontails were examined and tumors were found on 15. Tests for presence of neutralizing antibodies were made on sera of 36 of these 86 rabbits and 16 were found positive. Using both procedures, 26 (30%) gave evidence of past or present infection with the fibroma virus. Of 36 cottontails examined between July and December, 1951, 19 either had visible tumors or were positive for neutralizing antibodies (52.8%). In 1952 blood sera were collected only in April from 2 rabbits; one was positive for neutralizing antibodies. In 1953, tests were made on sera from 9 rabbits: two collected in March were negative for neutralizing antibodies; of two collected in June, one was positive; and, of five collected in November, one was positive.

TEST FOR SUSCEPTIBILITY OF OTHER WILD ANIMALS

Various animals were tested for susceptibility by intradermal inoculations of a strain of fibroma virus which had been isolated from a wild cottontail captured on the Refuge. Those subjected to the tests and encountered in the same habitats as cottontails, included 2 weasels (*Mustela frenata noveboracensis*), 4 opossums (*Didelphis v. virginiana*), 4 woodchucks (*Marmota m. monax*), 1 flying squirrel (*Glaucomys v. volans*), 6 white-footed mice (*Peromyscus leucopus noveboracensis*), 2 meadow voles (*Microtus p. pennsylvanicus*), 1 chipmunk (*Tamias striatus fisheri*), 6 bobwhite quail (*Colinus virginianus*), and 2 box turtles (*Terrapene carolina*). None of these animals became visibly ill and none developed lesions.

DISCUSSION

The significance of fibroma virus in rabbits is not known. Fenner (1953) has pointed out that myxoma and fibroma viruses, besides being closely related antigenically, are related in many other ways. Myxoma virus is highly fatal to *Oryctolagus cuniculus* but causes no lesions or apparent ill-effects in cottontails, although cottontails in Brazil have been indicated to be a source of infection for domestic rabbits. Myxoma is currently being used as an agent for the biological control of *Oryctolagus* in Australia and is decimating the population of rabbits in France and neighboring

[3] Animals made available by the Maryland Game and Inland Fish Commission.

countries after a single plant on an estate near Paris.

Fibroma can be transmitted readily to either *Oryctolagus* or *Sylvilagus*. *Oryctolagus*, after treatment with the fibroma virus, is immune to the myxoma virus. It has also been demonstrated (Berry and Dedrick, 1936) that the fibroma virus can be transformed into the myxoma virus. The pathogenicity of myxoma in *Oryctolagus* and the fact that myxoma has close biological relationship to the fibroma virus make further study of the latter in our native cottontails a desirable project.

There have been few studies relating to the incidence of fibroma in cottontails. Haugen (1942), in his studies on cottontail rabbits in southwestern Michigan observed 40 cases of skin tumors, all occurring between September 1 and December 13. Although he reported these as papillomas, his description of the tumors and subsequent studies indicate he was observing fibromas. He noted that all but two of his infected rabbits were definitely less than one year old. Haugen reported that three rabbits which had tumors in the fall of 1938 had no evidence of these growths when recaptured in the summer of 1939. Tumors evidently disappeared from infected rabbits during winter.

Reilly (1954) reports fibroma on 8.6 per cent of 174 cottontails from the Three Rivers Game Management Area, Baldwinsville, N. Y., in 1953. The most extensive published data on incidence of fibroma in wild cottontails are to be found in the annual reports of the Rose Lake Wildlife Experiment Station (1940-1945). Tumors were first noted there in 1940-41 but no incidence data were given. In 1941-42, 3 of 95 cottontails examined during July-August, were found infected; 10 of 147 examined between September 11 and October 10 had fibroma; no tumors were observed on 51 rabbits inspected in January and February; and, none were found on 32 rabbits taken in March and April. In the fall of 1942, fibromas were observed on 21 of 224 rabbits trapped.

In 1943, no fibromas were reported on 13 rabbits handled between April 1 and June 30; but tumors were present on 5 of 55 examined during the period July through September and on 7 of 112 captured between October and December inclusive. The original report (1943) also stated that of 99 rabbits examined during the hunting season, October 15 - December 31, only one had fibroma. During 1944, no fibromas were found on 30 rabbits examined from April 1 to June 30, and none were found in that year on 55 examined during the pre-hunting season trapping. Only one rabbit of 158 examined during the hunting season showed evidence of fibroma. A single rabbit with fibroma was observed in 1945.

In comparing the Rose Lake findings with those obtained at the Patuxent Research Refuge it is evident that there was a higher incidence of fibroma in the Patuxent cottontails in 1951 than in the peak years of the infection at Rose Lake in 1941-43. Although the number of rabbits examined since 1951 is small, lack of any evidence of tumors in 223 rabbits collected in several previous years seems to indicate that there was an epizootic of fibromas at the Patuxent Research Refuge. The same seems to be true for Rose Lake although a low grade enzoicity is also indicated by the occurrence of a single case in 1944 and again in 1945.

Rabbit populations at the Patuxent Research Refuge have gone from a comparatively high level during 1947 to 1951 to a low in 1952 and 1953. There was a drop from an average of 8 to 12 or more animals per 100 acres during 1947-1950 to less than one per 100 acres in 1953. These last two years marked the completion of an extensive brush removal program in areas which served as source of specimens.

So many problems can be involved in population fluctuations among wildlife that it becomes difficult to demonstrate any single factor as a prime cause. Fibroma-infected animals have been readily maintained in captivity without mortality. Infected rabbits, when retrapped, showed complete regression of tumors. (Haugen and present study). Currently, there is no evidence that fibromas affect population density of cottontails.

According to present knowledge, hunters need have no fear concerning handling or eating rabbits with fibroma. The tumors are confined to the skin and are automatically removed when an animal is pelted. There is no evidence of transfer of the infection to man either through handling or eating rabbits which have been infected with these tumors.

SUMMARY

Between March, 1947, and December, 1953, 359 cottontails were examined for evidence of fibromas at the Patuxent Research Refuge, Laurel, Md. No tumors were observed on the rabbits until December, 1950, when 3 of 16 shot animals had fibromas. Twelve rabbits of 70 examined in 1951, had tumors and no tumors were found on 37 examined in 1952 and 29 examined in 1953.

Neutralization tests, using Shope (OA) fibroma virus, were positive on sera from 6 of 36 rabbits trapped between July and December, 1951; one of two rabbits tested in 1952 showed evidence of antibodies; and 2 of 9 tested in 1953 were positive. Neither fibromas nor circulating antibodies were found in 70 cottontails trapped in January and February, 1953, in Rockville, Maryland and over 30 cottontails obtained from dealers in Kansas and Arkansas. No lesions developed on several species of mammals inoculated with a strain of the fibroma virus isolated from a wild cottontail captured on the Refuge.

These findings were interpreted as indication of occurrence of an epizootic during the period December, 1950 through December, 1951. Although the local cottontail population showed a marked drop following this epizootic, available data were insufficient to determine whether or not fibroma virus was a contributing factor.

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FILARIAE IN A WINTERING FLOCK OF CANADA GEESE

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In a study of blood smears from 353 Canada geese (*Branta canadensis interior*) at the Horseshoe Lake Game Refuge, Illinois in November and December of 1950, Levine and Hanson (1953) found microfilariae in 4 birds (1.1%). Two species were encountered. A long form measuring 323 to 341 by 4.0 to 4.4 microns was found in one bird, and a short form measuring 50 to 82 by 4.0 to 4.4 microns in three birds. In the winter of 1953-54, a second survey was carried out by the senior author on 306 Canada geese wintering at the Horseshoe Lake Game Refuge. The results of this survey and of laboratory studies in Urbana by the junior authors are reported here.

For close cooperation in the goose trapping program we are indebted to George C. Arthur of the Illinois Department of Conservation.

METHODS

The geese reported upon were trapped between November 2, 1953 and February 13, 1954. Blood examinations were usually made within a day of capture of the geese, the time of observation being between 9:00 a.m. and 6:00 p.m.

Blood was obtained by puncture of the brachial vein. A drop of blood was placed on a microscope slide by touching it to the small pool of blood resulting from the puncture. It was immediately covered with a coverslip, and examined under the low power of the microscope for about 3 minutes. Usually the perimeter of the preparation was examined first, and this was followed by random examination of the central portion.

The birds were divided into juveniles, yearlings and adults on the basis of tail feather and cloacal characters (Hanson, 1949). The juveniles were estimated to be 5-8 months old and the yearlings 17-20 months old at the time of examination.

A number of the most heavily infected geese were held in captivity for laboratory study and autopsy.

RESULTS

SPECIES IDENTIFICATION—The filariae reported from Anseriformes have been reviewed by Levine and Hanson (1953) and Anderson (1954). Since no adult filariae had been described from Canada geese, Levine and Hanson (1953) did not attempt to assign scientific names to the two forms of microfilariae which they found. Work reported in the present paper makes it possible to do so positively for one species and tentatively for the other.

In an unpublished survey of the helminths of Canada geese carried out in cooperation with the Illinois Natural History Survey, James Gilford found adult filariae in the heart muscle of a number of Canada geese. These have been identified by E. E. Wehr, J. C. Gilford and C. M. Herman (personal communication) as *Sarconema eurycerca*, which was originally described by Wehr (1939) from the whistling swan, *Olor columbianus*. Other specimens submitted by us have been identified by Dr. Wehr as belonging to the same species.

Twenty-seven "long form" microfilariae were found in the blood smear of an adult bird on January 28. On February 5 this bird was sacrificed and autopsied. A total of 14 adult *S. eurycerca* were found in the myocardium. Four were visible just under the epicardium, one was just under the endocardium, and the other 9 were deep in the myocardium. In blood taken from the auricles at autopsy, 28,000 microfilariae per ml. were found.

An adult female *Sarconema* from this bird was teased apart, and long form microfilariae were found in it. The identity of this form is therefore established.

The general morphology of the microfilariae of *S. eurycerca* has already been described by Levine and Hanson (1953) and by Anderson (1954). However, in these papers it was stated that the microfilariae had no sheath. None could be seen in the Giemsa-stained preparations on which these descriptions were based, but a sheath was found in wet mounts of microfilariae both from the peripheral blood and directly from the adult female. It extended some distance anteriorly and posteriorly, and was easily visible under both phase contrast and standard microscopes. No oral stylet was seen.

Six Canada geese with many "short form" microfilariae in their peripheral blood were sacrificed and examined carefully. No adult filariae were found, although the examinations consumed several hours each, and the tissues and organs were teased apart minutely. The birds were skinned completely before examination, and the skin, esophagus and intestines were examined both by transmitted and reflected light.

Since this work was done, Anderson (1954) described *Ornithofilaria fallisensis* from the subcutaneous tissue of White Pekin ducks (*Anas boschas*) at Algonquin Park, Ontario, Canada. Anderson stated (*in litt.*) that the adult filariae were extremely difficult to find, especially if the birds were fat, and that he had found it helpful to starve the ducks for a week or two previous to autopsy. Anderson (1954) described the microfilariae of *O. fallisensis* in detail. They differed from the short form described by Levine and Hanson (1953) from the Canada goose in that they had a sheath. However, Anderson examined Giemsa-stained slides which we sent him, and stated that although

a sheath could not be detected on our microfilariae they were apparently like those of *O. fallisensis* in other respects. Anderson reported finding the sheath in his *O. fallisensis* microfilariae after staining intravitally with azur II-eosin, but found it in only a few stained with Giemsa or methyl green-pyronin. In the present study no sheath was seen on the short microfilariae from the Canada goose, but they were examined only while alive or after staining with Giemsa.

The descriptions of the microfilariae given by Levine and Hanson (1953) and Anderson (1954) will not be repeated, but additional observations made on living specimens with the phase contrast microscope are of interest. An oral stylet was present; it was alternately protruded and retracted from the mouth. Two pulsating structures were seen within the body. One was the excretory ampulla, which lay about 1/4 of the body length behind the anterior end. The other, which lay about 1/4 of the body length from the posterior end, looked very much like the excretory ampulla, but discharged thru the anus.

It is quite likely that further study will show that the Canada goose form is actually a species of *Ornithofilaria*, if not *O. fallisensis*. For the present it is designated *Ornithofilaria* (?) sp.

INCIDENCE OF MICROFILARIAE—Microfilariae were found in 23.9% of the 306 Canada geese examined in this study. *S. eurycerca* was present in 2.9% and *Ornithofilaria* (?) sp. in 21.6%. Two birds had double infections. This incidence is almost 22 times that reported by Levine and Hanson (1953) in their 1950 survey, and reflects the much greater efficiency of the present technic. In the earlier survey the main interest was in blood protozoa, and thin stained smears were examined for 10 minutes under the oil immersion objective. In the present survey, thick, wet smears were examined for about 3 minutes under low power (100 x). In most cases one to three microfilariae were seen in a wet smear, but up to 27 *S. eurycerca* and 26 *Ornithofilaria* were seen in different smears of peripheral blood.

The relation of age of the geese to incidence of microfilariae is given in Table 1. Strikingly different pictures were obtained with the two species. The incidence of *Ornithofilaria* was highest (28.8%) in the juveniles, and fell to 21.4% in the yearlings and 11.7% in the adults. This decrease in incidence suggests the development of some immunity with age.

TABLE 1.—RELATION OF AGE TO INCIDENCE OF MICROFILARIAE IN CANADA GEESE AT HORSESHOE LAKE GAME REFUGE, WINTER 1953–54

Age Class	Number Examined	Per Cent Positive *Sarconema eurycerca*	Per Cent Positive *Ornithofilaria* (?) sp.	Total
Juvenile (5–8 months old)	153	0.0	28.8	28.8
Yearling (17–20 months old)	42	9.5	21.4	31.0
Adult (29 months and older)	111	4.5*	11.7*	14.4*

* Includes 2 birds with double infections.

Sarconema eurycerca microfilariae were found in 9.5% of the yearlings and 4.5% of the adults. This decrease in incidence also suggests the development of some immunity.

No *Sarconema* microfilariae were found in any of the juveniles. There are two possible explanations for this. One is that the birds are infected with both species of filariae in their northern breeding grounds and that the prepotent period of *Sarconema* is so long that microfilariae do not appear in the peripheral blood until after the birds are more than 7 or 8 months old. A second explanation is that they are infected with *Sarconema* in their southern winter quarters.

SURVIVAL OF MICROFILARIAE—In connection with these studies, some incidental observations were made on the survival of the microfilariae in serum. The blood was usually obtained from the heart at autopsy, allowed to clot, and the serum was placed in a cotton-stoppered test tube and stored either at room temperature or in the refrigerator at approximately 5°C. It was then examined periodically for motile microfilariae. Under these conditions, *Sarconema eurycerca* microfilariae survived in the refrigerator for 38 days and *Ornithofilaria* (?) sp. microfilariae for 25 and 34 days, respectively, in two tests. At room temperature the *Ornithofilaria* microfilariae survived 7 days.

SUMMARY

Microfilariae of *Ornithofilaria* (?) sp. were found in the blood of 153 juvenile Canada

geese, 21.4% of 42 yearlings and 11.7% of 111 adults at Horseshoe Lake Game Refuge, Illinois in the winter of 1953-54. Microfilariae of *Sarconema eurycerca* were found in none of the juveniles, 9.5% of the yearlings and 4.5% of the adults. The microfilaria of *S. eurycerca* was found to have a sheath, and that of *Ornithofilaria* (?) sp. to have a protrusible oral stylet. The microfilariae of *S. eurycerca* survived 38 days in serum at 5°C., while those of *Ornithofilaria* survived up to 34 days at 5°C. and 7 days at room temperature.

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REVIEWS

North American Moose. By Randolph L. Peterson. University of Toronto Press, Toronto, Canada, and Oxford University Press, London. In cooperation with the Royal Museum of Zoology and Paleontology. i–xi, and 280 pp. 66 Figs. (including 44 photographs) and 35 tables. 1955. $12.50.

Here we have for the first time a scientific study of moose, in all its habit and ecological aspects, on a wide continental basis. Mr. Peterson did his personal, detailed investigations in Ontario over a period of years ". . . from 1946 on." There have been some intensive studies of moose on a smaller geographic scale, notably on Isle Royale, Michigan. Mr. Peterson has used all such published data and, correlating them with his own findings in Ontario, has presented us with a remarkably thorough life history and evaluation of moose life in North America.

In the Old World he lists the basic species of Europe, *Alces alces alces*, the European elk; *Alces alces cameloides*, Manchurian elk, whose taxonomic status seems uncertain; and *Alces alces pfizenmayeri*, the Siberian elk. In North America we have four moose: *Alces alces gigas*, the large Alaskan moose; *Alces alces shirasi*, the Yellowstone moose of the Rocky Mountain region from Wyoming northward into southeastern British Columbia and southwestern Alberta; *Alces alces andersoni*, the northwestern moose, of northern Michigan and Minnesota, western Ontario, and north to the Mackenzie Delta; and *Alces alces americana*, our eastern moose. A series of maps gives the moose distribution with reference to the North American glaciation, and Mr. Peterson discusses the animal's paleontological history. The author also gives the distribution and population status state by state and province by province, and gives special attention to Ontario, where he did much of his work. Then he discusses in detail the reproduction and general life history and behaviour of the moose. The food habits in particular are treated fully and there are chapters on habitat, relations with other animals, diseases etc., and management.

Mr. Peterson discusses the movements of moose. We are of course familiar with the invasion of new territory by a moose population, such as happened in part of British Columbia in the 1930's, and migration in mountain country, such as the mass movement to lower willow country for winter, in Jackson Hole. Also, as the moose population became over-large in western Wyoming, some of the moose were known to move out on the sagebrush plains in winter, where they browsed on desert shrubs. On the whole, however, food being adequate, the moose is a sedentary as well as comparatively solitary animal. On one occasion we had under observation for five days a bull moose, in summer, which stayed in a very small patch of willows, not moving more than one hundred yards except to go to a nearby creek for a drink. And in Jackson Hole moose come to certain ponds in summer to feed on aquatic vegetation, so regularly that visitors to Teton National Park can almost plan to find moose in "the moose ponds" every evening.

Mr. Peterson mentions reports of moose feeding on grass and kneeling to do so. On several occasions in Yellowstone Park my brother and I have seen moose kneeling to feed in that manner.

This book contains an excellent chapter on food habits. The author considers the willow the most important food plant and this is well borne out by the facts. Of course, in part of the northern forest balsam is very palatable. In the Rocky Mountain area other firs are equally palatable and on heavily

stocked winter ranges all the young firs of several species are closely cropped as well as older limbs within reach. I believe we can say that all firs are palatable to moose.

But in much of the western range, from Wyoming to interior Alaska, willow is the standby. Such species as the aspen, cottonwood and fir are palatable, but the moose soon eats the twigs within reach, and thereafter the production of food is very limited, while the willow is all within reach and recuperates well. Perhaps it can be said that in the west the permanent distribution of moose is pretty well defined by the distribution of extensive willow growth.

I know that it has so often been reported, but I must confess that I have never seen a moose "ride down" a sapling to reach its upper branches, nor have I seen the sign that would indicate it. But I have seen moose reach up in cottonwoods and tall willows, seize a limb in its teeth and with a sidewise pull break the limb, and then proceed to feed on the tips of the drooping branch. In fact, a much used winter range in willows can be recognized not only by the stubby browsed twigs, but also by the numerous dead limbs of the taller bushes, drooping down at odd angles.

"North American Moose" is our number-one treatise on this animal. The author has painstakingly searched all the literature and with his own detailed field work has produced a volume that contains what we know about this subject. Our conservation of wildlife today depends on intelligent management. For this we need facts. This book has them. For anyone concerned with management this is truly a guide.—OLAUS J. MURIE.

Plant for Vildtet (in Danish, Wildlife Plantings). By C. Syrach Larsen. J. H. Schultz A/S, University Press, Copenhagen, 1952.

This paper presents some interesting information about the status of wildlife plantings in Denmark. It is described that while formerly game was reared and protected mainly on the big estates, now only few of these large domains remain and that it is now the responsibility of the average land owner to plant to aid game, especially because hedges have become much scarcer. The author advocates the planting of shrubs in preference to trees, as they are much more useful to wildlife. He also suggests that even small areas, such as gravel pits, be planted.

Larsen advises the selection of those species which are most suitable for local soil and climatic conditions and presents a list with recommendations regarding site requirements and other details. The following species are mentioned as most important: *Prunus spinosa, Crataegus monogyna, Hippophaes rhamnoides, Lycium halimifolium, Rosa rugosa, Ulex europaeus, Sarothamnus scoparius.*

The planting of one or more species belonging to the following genera is also recommended: *Rubus, Corylus, Sambucus, Prunus, Lonicera, Syringa, Ligustrum, Ribes, Pyrus, Sorbus, Rhamnus, Juniperus, Myrica, Salix, Fagus, Betula, Alnus, Pinus* and *Picea.*

It is interesting that the Danes capitalize mainly in indigenous species, an approach which may be looked into somewhat further on the North American continent.—ANTOON DE VOS.

BRIEFER ARTICLES

NOTES ON THE SEX RATIO OF GAMBEL'S AND SCALED QUAIL IN NEW MEXICO

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The authors (1953. Studies on quail malaria in New Mexico and notes on other aspects of quail populations. Dept. of Game and Fish, Santa Fe, 79 pp.) have pointed out the previously known fact that, at least under natural conditions, males apparently outnumber females in both Gambel's quail (*Lophortyx g. gambeli*) and scaled quail (*Callipepla squamata pallida*). The figures for wild populations in New Mexico as a whole were as follows: Gambel's quail, 107.2 males per 100 females (788: 726); scaled quail, 104.3 males per 100 females (293: 281). Since age classes were not separated, no light was thrown upon the question of whether the uneven sex ratio results from differential mortality, from an original difference, or from both. Part of our data have been re-examined to take the age factor into account.

The sex ratio at hatching and in juveniles does not appear to be known, and we have no data on these points. The so-called "immatures" and "adults" are, therefore, the only age classes considered. The "immatures" are birds approximately 3 to 18 months old, and the others are older birds which have completed their first post-nuptial molt. We feel that "immature" is a misnomer for an age class which, in quail, probably normally constitutes well over 50 per cent of the breeding population. Hence, this whole group between juvenile birds and

fully adult birds is referred to in this paper as "young-adult." We call the other group "full-adult." These age classes are readily separated in both species by differences in color and pattern of the upper primary coverts.

Our data show the sexes in the two age classes to be distributed as follows:

Gambel's quail: young-adult, 105.9 males per 100 females (270: 255); full-adult, 126.3 males per 100 females (120: 95).

Scaled quail: young-adult, 90.2 males per 100 females (101: 112); full-adult, 143.1 males per 100 females (83: 58).

We interpret these results to mean that, under natural conditions, a definite sex-differential mortality occurs, favoring males, in both Gambel's and scaled quail. Apparently, females do not fare as well as males in the struggle for survival. This probably accounts for the observed difference in relative numbers of males and females in the wild, although our data do not absolutely rule out the possibility of an original difference.

The anomalous sex ratio noted for young-adult scaled quail almost certainly resulted from errors in sexing the birds. Live scaled quail are routinely sexed on the basis of slight differences in the color of the throat feathers. Ideally, in males these feathers are clear buffy, while in females they are grayish with faint longitudinal brown streakings. In full-adults these differences are usually very evident to a practiced eye. In young-adults, however, they are less definite and more variable, tending in general toward the female condition. This no doubt causes many errors in sexing scaled quail of this age class. That it is possible, nevertheless, to sex this species accurately by the method mentioned is indicated by the fact that one of the authors, after he had acquired several years experience sexing scaled quail, sexed a test series of 17 live birds without a mistake, as subsequently confirmed by dissection. Eleven of these were young-adults.

Due to obvious differences between males and females in Gambel's quail of all ages except quite young birds, this species can be accurately sexed.

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A FIELD TECHNIQUE FOR BURSAL INSPECTION OF MOURNING DOVES[1]

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A technique of aging doves by feather characters (Pearson and Moore 1940) involves the inspection of wing feather tracts to determine the presence or absence of white-tipped primary coverts, indicative of juvenile doves. This method is in common use in states where doves are hunted. The author found that this feather character loses some of its reliability by the time the post-juvenile primary molt has progressed to the eighth primary. It was found that a few juvenile doves molting to the eighth primary showed no white-tipped primary coverts, and those juvenile doves molting the ninth or tenth primaries seldom exhibited white-tipped coverts. For this reason, the presence or absence of the bursa proved to be the only reliable indicator of age among doves that had molted the eighth, ninth, or tenth primaries, and lacked white-tipped primary coverts.

Field inspection of the hunter's bag involves separating out the obvious juveniles by the presence of white-tipped primary coverts. The obvious adults, which have molted Primaries 1 to 7, are then separated from doves of questionable age, having molted Primaries 8 to 10. Doves of this latter group require bursal inspection for accurate age determination.

The following field technique for the determination of the presence or absence of the bursa is rapid and should not prove objectionable to the dove hunter. That portion of the dove's tail that is removed has no valuable edible qualities.

A transverse cut is made immediately posterior to the vent. Materials needed for this dissection include a heavy pair of shears; the type commonly termed "boning shears," with serrated cutting edges, are especially suitable for this purpose. Prior to making the cut, a few of the upper and lower tail covert feathers are removed to expose the vent and the preen gland. The dove is then held on its back, and the shears are placed immediately behind the posterior lip of the vent. The cut is made as close to the vent as possible, without cutting into the cloaca. Figure 1 indicates the proper placement of the shears for this cut. The cut is made completely through the tail, severing the pygostyle. The severed portion of the tail is discarded, and the dove is examined for presence of bursa. The bursa, if present, is found immediately dorsal to the vent. It is a round yellow structure having fine vermiculations and is unlike any other

[1] This study is a contribution from the Pittman-Robertson Dove Research Project 13-R-8, of the Missouri Conservation Commission.

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FIG. 1. Position of shears for severing tail of mourning dove to expose bursa. Shears are placed posterior to the vent (A) but as close to it as possible.

FIG. 2. Bursa (B) in juvenile mourning dove exposed by cut by shears. C—Bursal opening located just beneath the dorsal edge of the lip of cloaca.

tissue exposed by this cut. It is 10 to 12 mm. long and 6 to 8 mm. wide, and is readily discernible. (Figure 2.)

An alternate method of bursal examination involves probing the bursa. Petrides (1950), in examining doves collected in Ohio, could find no opening in the dorsal wall of the cloaca leading into the lumen of the bursa. In the present study, the cloacal opening of the bursa was located without difficulty on the dorsal edge of the cloaca, just inside the dorsal lip of the vent. Probing of the bursa was a routine laboratory technique in this study, in classifying the questionable doves when age was obscured by the progress of the juvenal molt. This does not, however, represent a rapid field technique, as considerable time and care must be taken.

Use of the dissection method of field examination for presence or absence of the bursa is indicated as the most reliable method of aging doves whose primary wing feather molt has progressed to the eighth through the tenth primary, and has thus obscured the white-tipping of the primary wing coverts. Use of this technique permits rapid separation of this group into young and adult birds in the field.

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A DOOR CATCH FOR THE WOODEN BOX TRAP[1]

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Many who have used wooden box traps of the swinging door type have experienced difficulty from trap predation. In a recent field study of the Mearns cottontail four types of catches were used to hold the door closed. One of these catches proved very satisfactory. In three instances predators unsuccessfully attempted to enter the trap. One of the traps was moved end over end for 27 feet and the rabbit was still in the trap apparently unharmed.

The catch is made of strap iron, or other metal, about 1/16 inch thick, and with sufficient springiness to return to position after being slightly bent. It measures 1-1/2 inches by 5 inches and has 3 holes. One hole, 1/2 inch from one end of the catch is used for a screw to hold the catch to the bottom of the trap. A second hole, 2 inches from the end, is for an adjusting and holding screw. The release hole, 1/4 inch by 1/8 inch, is 3 inches from the end of the catch and is directly above a similar hole in the bottom of the trap.

One end of the catch is fastened to the floor of the trap and the other end of the catch is bent up, so that it must be forced down by the holding and adjusting screw. In this way the adjusting screw can be used to raise or lower the catch. This serves as an adjustment for the tension of the catch in case the sides of the trap swell and raise the door above the bottom.

When the released door drops, it depresses and slides over the catch, after which the catch springs up about 1/4 inch to its former position and behind the door to hold it closed.

A key is used to release the catch. The key is made by bending one end of a 3-inch piece of number 9 wire 180 degrees, 1/4 inch from the end. This bend forms a rectangular end which is 1/8 inch by 1/4 inch. The other end of the wire is bent at a 90-degree angle to form the handle. The key, which is inserted through the hole in the trap and catch, is turned 90 degrees and will not slip when the catch is pulled down. After the catch is released the door will swing open if the trap is set on end, and the catch springs back against the head of the adjusting screw after the key is removed.

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NEWS AND NOTES

WILDLIFE SOCIETY MEETINGS

The Council meeting will take place in the Jung Hotel, New Orleans, on Sunday, March 4, at 7:30 p.m. The annual business meeting will be held on Monday, March 5, at 8:00 p.m. The meeting rooms will be announced later.